DOCTORAL THESIS

Temporal and spatial patterns of dipteran and collembolan abundance in a Nigerian tropical forest canopy

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Temporal and spatial patterns of dipteran and collembolan abundance in a Nigerian tropical forest canopy

by

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Abstract

This study investigates the variation in the spatial patterns of Diptera and Collembola throughout the forest canopy due to seasonal changes in temperature and humidity in the monsoon climate of West Africa. There is a very distinct turnover in climate from the end of the dry season (the hottest and driest time of the year) to the beginning of the rains and this coincides with significant increases and decreases in the overall abundance of many forest dwelling Diptera and Collembola species. The study investigates spatial patterns on two gradients; vertically from the ground to the high canopy and laterally from the edge of the forest to the core, with the added complexity of the affects of anthropogenic burning of adjacent savannah. The results show that seasonality and the starting of the rains significantly affect both the overall abundance and the spatial patterns, providing species with a strategic change in habitat niche. During seasonal conditions that are less conducive to species' overall abundance, spatial patterns are suppressed by environmental conditions. However when environmental conditions are optimum for increased species abundance, spatial patterns are only suppressed by the availability of resources within the habitat (feeding or reproductive resources for example). Successive late burning events may have changed the structure of the forest edge introducing a significantly more open forest structure changing environmental conditions and thus creating a habitat more suitable for species which prefer lower humidity and higher temperatures.

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Chapter 1: Literature Review

There were many early attempts to access the canopy and study its various biological parameters. From binoculars and telescopes in the early nineteenth century (see Allee (1926)) to muslin traps hoisted into the canopy to investigate insects, birds and small mammals (Hingston, 1932), there were many innovations that early canopy explorers used to gain insight into a world that remained as yet little understood but a source of fascination for many. Sutton (2001) gives an excellent account of the early history of canopy science in a special eddition of Plant Ecology dedicated to canopy science, taken from the meeting of the European-Science-Foundation Canopy Research Programme, St Annes College, Oxford, UK, 1998.

More recently Lowman (2009) reviewed the innovations of the past 30 years of canopy research, and suggested likely foci of canopy research in the future. Lowman suggests that the using canopy research for not only research but also education and conservation will bring together a new generation of scientists that will help to establish this scientific field as the priority in ecological and whole forest interaction research.

This review will take each of the elements proposed for investigation in this thesis and examine the relevant literature. This thesis investigates how both temporal (seasonality) and spatial patterns (edge effects and vertical stratification) affect the abundance and richness of arthropod species within a tropical forest habitat. Therefore, as well as introducing the specific taxa to be investigated, this chapter will review past studies in temporal and spatial ecology, with specific references to arthropods.

1.1 Introduction

Western and Central Africa contains two main rainforest blocks (known as the Guineo-Congolian region), and is home to the second largest area of intact tropical forest, covering about 2 million km^2 (Duveiller et al., 2008). In order to maintain global biodiversity it is critically important that these forests are studied and conserved (such forests support 50% of Earth's terrestrial species (Dirzo and Raven, 2003, Ozanne et al., 2003)). Tropical forests are disappearing at an alarming rate, often through legal and illegal logging and the extraction of non timber forest products. Western Africa (all land mass west of an imagined north-south axis lying close to 10º east longitude) alone was believed to have lost 90% of its original primary forest vegetation by the end of the last century (Myers et al., 2000).

Within the tropical forest ecosystem there are many organisms that contribute to maintaining a functioning infrastructure. Arthropods are important members of this ecosystem, and play key roles in pollination, nutrient cycling and as detritivores. They act as food sources for numerous other organisms, for example, more than 50% of tropical Asian and Neotropical bird and bat species, and 30-40% of all non flying mammals are insectivores (Malcolm, 1997), and in Africa there are over 700 species of small insectivorous non-flying mammals (Nicoll and Rathburn, 1990). Arthropods are one of the most highly diverse and widely distributed groups of fauna in the world and therefore contribute to global ecosystem biodiversity. As arthropods are present in a diverse range of localised habitats throughout the tropical forest, the question of how species are distributed and indeed where their highest diversity occurs is key to understanding and maintaining effective ecosystem function.

The general premise of this thesis is the investigation of the spatial and temporal distribution of abundance and richness in Diptera (true flies) and Collembola (springtails) within a West African Guinean forest, designated as a 'Hotspot for Conservation' by Conservation International (see Myers et al. (2000) and Burgess et al. (2007)). Spatial patterns of diversity will be investigated on two gradients; the first is vertically from the forest floor to the crown of the canopy, and the second between continuous forest and forest edges (adjacent to both burnt and un-burnt savannah grassland). The temporal aspect of the research will look for differences in the spatial pattern of abundance and richness between the wet and dry seasons within the research area and along these gradients.

This study addresses arthropod abundance and richness at two scales; the micro-scale within and around a single living tree, and on the meso scale, between different contrasting environments. Ecosystem parameters can be measured on many scales from a space occupied by a single plant or sessile animal, to a local patch occupied by many individual plants or animals, right the way through to a biogeographical scale which can include areas of different climate (Krebs, 2001). Loreau (2010) states that in the past 50 years two distinct fields of ecological research have emerged; community ecology and ecosystem ecology, which have greatly influenced both theoretical and experimental studies. Community ecology is a bottom up approach that is concerned with species diversity and what factors increase or decrease diversity, whereas ecosystem ecology is a top down approach which focuses on the functionality of ecosystems as entities; how energy is gained, transferred and lost. Therefore this thesis will focus on aspects of community ecology. Loreau (2010) suggests a unified approach should be the aim of future investigations in the current age of massive biodiversity loss due to human induced

climate change; however, this falls outside the scope and resources of the present study.

This thesis will investigate the community structure, abundance and richness of two arthropod orders in a single space (namely a single tree and its surrounding vegetation), which in itself will be divided in to discrete height classes (from forest floor to canopy crown), and then compare between two spaces with different assemblages of forest structure (continuous forest habitat and forest edge habitat). The environmental factors incorporated into the experimental design will include aspects of forest structure and climate parameters as they change along horizontal (from forest edge to interior continuous forest) and vertical gradients. The study will also look at how anthropogenic activities (namely the burning of adjacent savannah grassland) affect these gradients both in terms of abundance and richness and habitat structure.

This research was undertaken at the Gashaka Gumti National Park in Eastern Nigeria (06°55' - 08°13' N and 11°13' - 12°11' E). The park is the largest in Nigeria, covering about 6600 km^2, and as well as being an important watershed, it is also home to a range of important flora and fauna. This area acts as an interface between the moist Cameroonian highlands (part of the Congo basin – 2nd largest area of tropical forest in the world) and the dry sub-Saharan Guinea savannah, and is therefore at the interface of Central and Western African forest habitats. The park is home to both large savannah vertebrates; such as elephant, lion and ungulates, and forest dwelling species such; as chimpanzees, black and white colobus and other primates in addition to over 500 species of birds and rare freshwater fish. As with many other forest habitats in Africa the park is under threat from logging, fire, overgrazing, poaching of non timber products, and the bush meat trade. So as this

park acts as a refuge and watershed, it important that sustainable long term conservation management is developed in order for the park to continue to provide key ecosystem services to not only the wildlife but the local human population that depends on the area for their livelihoods. By analysing the community structure and diversity of Collembola and Diptera in both continuous and edge (burnt and non burnt) forest habitat it will be possible to assess the impact that savannah burning and anthropogenic habitat management has on the communities of these two arthropod orders.

1.2 Focal Taxa

Diptera and Collembola have been chosen as the focal taxa for this study as they contribute to key ecosystem services. Collembola are small bodied hexapods, <12 mm in length, and one of the most widely distributed animal groups on the planet (with populations found in snow fields, tropical/subtropical/temporal/boreal soils, canopies, forests, caves, grasslands and inter-tidal zones) (Hopkin, 2007). Collembola are involved in nutrient cycling and decomposition, living primarily in soil and leaf litter, and found in foliage, bark and freshwater (Hopkin, 2007). The Collembola also provide food resources for a number of other organisms such as Acari (mites) and Araneae (spiders).

Diptera are also found in a variety of habitats from boreal to tropical environments. They function as pollinators, detritivores and as disease vectors. There are some 240,000 estimated species of Diptera with roughly 120,000 species described to date. They feed on a variety of food resources including plant matter, detritus, carrion and live organisms (parasitic/parasitoid/blood suckers) (Stubbs and Chandler, 1978).

Like the Collembola the Diptera inhabit a wide variety of habitat niches within forests and are therefore excellent indicators of habitat heterogenity and diversity.

1.2.1 Diptera

This study aims to investigate how habitat structure and anthropogenic management affect habitat quality, using both Diptera and Collembola as bioindicators of habitat heterogeneity and diversity. Many arthropods have been used in past studies as bioindicators, for example, ants, Lepidoptera, carabid beetles, cerambycid beetles, dung beetles, spiders, syrphid flies and parasitic wasps (Maleque et al., 2009, van Straalen, 1997). Detection of possible indicator species has been developed through the use of analytical tools such as the Indicator Value (IndVal) method (see McGeoch et al. (2002) for an example of its use), as conventions such CBD (Convention on Biological Diversity, 1992) have emphasised their use in conservation practise. Previous studies specifically investigating Diptera as bioindicators are dominated by studies of freshwater quality and climate change using families such as chironomidae (see Hamerlik and Bitusik (2009); Simiao-Ferreira et al. (2009) for examples). There are also some studies using syrphid flies as indicator species to determine habitat change in agricultural systems and plantation forests (Sommaggio, 1999, Smith et al., 2008a).

To test the indicator value of the Diptera as a measure of habitat heterogeneity and diversity da Mata et al (2008) used drosophilid assemblages to measure human disturbance in forests, savannah and urban environments, and compare the results to that of undisturbed forest. The authors proposed this particular family of Diptera as there are few other arthropod families with more available information regarding their taxonomy, ecology and physiology. Additionally, until this study, Drosophilidae had only been proposed as bioindicators for forest disturbance and not

fully tested (Ferreira and Tidon, 2005). This family has been shown to respond to variability in microclimate, forest structure and complexity at the community level, with distinct differences in community between primary and secondary forest (Tanabe et al., 2001, Ulyshen, 2011). Da Mata (2008) sampled four habitats, namely undisturbed gallery forest, disturbed gallery forest, undisturbed savannah and an urban environment. The results of the study showed that the drosophilid assemblages were good indicators of habitat variability.

The undisturbed forest supported the greatest number and dominance of Neotropical and narrow range (species that occurred in <16 sites) species, whereas widespread and exotic species dominated the disturbed forests, savannahs and urban environments. With the current need to determine and measure the productivity of tropical habitats this study represents a good indication that drosophilid (and perhaps Diptera as a whole) are worthy indicators of habitat disturbance. However this work was only possible due to the wealth of current knowledge of the drosophilid family.

Knowledge of West African dipteran families is dominated by studies of Diptera as disease vectors and/or their control. A simple search in the online reference database Web of Knowledge , on the terms “Diptera” and “West Africa” as search parameters demonstrates this case. The search returned 312 results, with subject areas such as infectious diseases (n=163), public, environmental and occupational health (n=105) and parasitology (n=51) (total n=319, note that each article is tagged with more than one subject area within this database). By contrast "zoology" plus "West Africa" returned n=86 and "biodiversity" and "conservation" returned n=33. This shows that the emphasis of the current research on Diptera in West Africa is clearly concerned with the spread of disease and not zoology, biodiversity or indeed taxonomy. Therefore if a similar study to that of da Mata et al (2008) was to be conducted in

West Africa it may be necessary for families such as Glossinidae (tsetse fly – trypanosomosis vector) or the culicidae (containing the *Aedes* - yellow and dengue fever vector, and *Anopheles* - malaria vector, mosquitos) to be used instead of the drosophilids.

Jardine et al. (2008) investigated the use of culicidids, or more specifically, the spread of malaria as and environmental bioindicator. They concluded that although the increase in malaria in certain areas does sometime indicate an increase in human induced habitat degradation the results are often insensitive and therefore must be combined with other environmental factors. However from an environmental perspective the use of families such as culicidae as bioindicators does now have a precedent.

This highlights one of the major problems with the study of many arthropod groups in West Africa, which is that there is very little information or taxonomic verification of species in this biogeographical region. Therefore, as with other studies referenced in this chapter, it will be necessary to identify to either morphospecies or to family/genera rather than their full taxonomic description, as it is likely that they will be poorly known groups or new records to science.

Throughout this chapter there are references to the effects of temperature, humidity and rainfall on invertebrates. Through investigation of plant pollinator relationships, several studies have observed that Diptera play an important role in wetter and cooler environments. Studies from higher latitudes observed that Diptera replace bees as insect pollinators in habitats where rainfall is higher and temperature lower (Devoto et al., 2005). Additionally in more tropical latitudes when studying plant pollinator

relationships along rainfall, humidity and temperature gradients, Diptera replaced bees as dominant invertebrate pollinators (Gonzalez et al., 2009).

Janzen and Schoener (1968) showed that there was a definite shift in bee and dipteran populations between the wet and dry seasons. The author attributed this to Dipteran morphology and life history traits which allowed them to be less susceptible to more adverse weather conditions. Diptera need less energy intake during the day than bees. As bees need to maintain nest structure and feed multiple offspring which means that they require much higher levels of energy intake and must therefore forage for much greater lengths of time. Other problems associated with bees' maintenance of nest during wetter periods stem from increased infection rate of bacteria and fungus in the nest due to higher humidity. Diptera do not have these problems; in fact many species require standing water to lay their eggs in, with subsequent offspring spend their first few instars living in the water. Most Diptera do not invest energy into offspring survival, eggs and larvae are left to fend for themselves relying on large numbers of eggs to maintain population levels.

1.2.2 Collembola

West African Collembola are represented in the literature, although there is still an emphasis on studies with a higher economic impact, such as agriculture; however there are some ecological studies and in fact agricultural studies that have relevance to the present study. There are also examples that can be taken from other areas of the world.

One of the main exponents of Collembolan studies in Nigeria has been the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. One such study from the IITA by Badejo et al (1998) looked specifically at the abundance of

Collembola under four different agroforestry tree species as well as secondary forest and grassland, and measured the changes in abundance over a one year period. Although the results from the specific test of tree species are in some ways relevant, information regarding the effect of soil temperature and moisture is critical to understanding the effects of temporal change in Collembola abundance across tropical habitats. Bedejo et al (1993) showed that Collembola were positively correlated with soil moisture and negatively correlated with soil temperature. This means that during the dry season there is a significantly lower abundance of Collembola than in the wet season. The difference in abundance between the wet and dry season was quite dramatic. Dry season pitfall traps from the secondary forest and grassland sites yielded fewer than 100 individuals per sample; where as in the wet season up to 100,000 individuals were found in each trap. However the abundance derived from soil cores (0.006 m^2) was much lower, with abundance ranging from 0 (Feb, March, Dec and Jan) to 26 per sample (4333 per m^2) (April) for the three co-dominant genera (*Isotomodes*, *Tullbergia* and *Cryptopygus*) in the secondary forest plots. The study also showed that grassland and secondary forest habitats had the highest variability of Collembola abundance, which is probably due to the heterogeneous structure of the habitats.

Badejo et al (1993) showed that Collembolan abundance was significantly influenced by soil moisture content and soil temperature in a tropical environment. There are, however, other factors that may influence their populations, aspects such as resource availability and predator-prey relationships. Ferguson & Joly (2002) wanted to ascertain if Collembolan populations were regulated by density, predation or weather in a temperate environment. Through a series of field collections and manipulations they concluded that there was no top down control (specifically predation by mites) and that resource availability and temperature played a much more significant role in

determining population density. This further supports what Badejo et al (1998) showed in their study, that the environment has a very significant influence on Collembolan abundance, and that due to their small body size and exothermic nature, environmental factors will always play a larger role in their population abundance than trophic parameters.

So far the studies discussed here have all shown that temperature, soil moisture and food resources are the controlling factors in Collembolan abundance. Other studies such as Palacios-Vargas et al. (2007), Huhta & Hanninen (2001) and Usher (1970) have also drawn similar conclusions about the association of Collembola population density and abundance to their surrounding environment in both temperate and tropical habitats. However Irmler's seven year study of a North German Beech forest (2006) showed only a weak significant effect of two parameters (July precipitation and mean annual temperature) which shows that there may also be site specific effects on collembola density. The site that Irmler used was a relatively new (less than 100 years old) beech forest, where beech was the only tree species present, and had previously been an agricultural field. This is therefore a young and relatively homogeneous habitat compared with the African woodland under study, with reduced niche microhabitat for colonisation. Therefore the site itself may have a lower abundance and diversity of collembolan species as compared to a more heterogeneous environment. However, with perhaps the exception of Irmler (2006), most studies find that Collembolan population dynamics are dependent on environmental factors rather than trophic influences.

With the above studies mostly concluding that environment plays an important role in Collembola population dynamics, what would happen if the environment was changed, e.g. habitat conversion, deforestation or in fact reforestation? Ponge et al.

(2006) investigated the effective dispersal of Collembola. The authors split species into fast and slow dispersing species, based on morphological characteristics. Fast dispersing species were classified by having fully developed jumping organs, long legs and eight ocelliper per eye patch (complete visual apparatus), whereas slow dispersing species had short legs, under developed or no jumping organ two or fewer ocelliper per eye patch . The study concluded that most slow dispersing species inhabited forest habitats whereas fast dispersing species predominantly inhabited grassland habitats. The authors therefore concluded that rapid habitat conversion would not allow most forest dwelling species of soil associated Collembola to disperse and find refuge. Shaw (2003) investigated successional colonies of Collembola at a brown field site in the UK and found that as the habitat progressed from wasteland to forest that the later forested colonies were white eyeless species of the deeper soil layers similar to the slow dispersing forest species that Ponge et al. (2006) describe.

The literature indicates that Collembola are negatively affected by habitat change; however it has also been shown, at least in temperate environments, that fragmentation and isolation have little effect on soil micoarthropods. Schneider et al. (2007) conducted isolation experiments on soil microarthropods (including Collembola) to ascertain if there were changes in density and abundance caused by this manipulation. The results of the study showed that over a sixteen month period that isolation had no significant effect on the soil Collembola. The authors believed that the niche habitat size was so small for these organisms that being cut off from connecting habitat had little or no effect. The experimental design did not, however, allow for immigration into the isolated patches, which means that potential competitors or predators were not allowed into the system.

The conclusions that can be drawn from the literature above are that Collembola are sensitive to variations in temperature and moisture, which in the context of this study is very important. As has been stated elsewhere in this chapter, the horizontal and vertical gradients that are being studied in this present investigation cause such changes in the temperature and moisture (among other factors), therefore it would follow that there should be a detectable effect in Collembola abundance/diversity seen along these gradients. Therefore it will be necessary to quantify these gradients within the study site.

1.3 Vertical stratification

The concept of vertical stratification is one that has its basis in the same phenomenon as the effect of forest edges. Edge effects are explained in section 1.4 but the basic concept is the same. As the habitat proceeds from the forest floor into the uppermost layers of the canopy where the vegetation interacts with the atmosphere, the microhabitats produced by changes in environmental factors and the resulting changes in vegetation structure and mass give way to a variety of habitat niches that are not found on or near the soil horizon. It is therefore applicable to classify the forest crown, the interface between vegetation and atmosphere, as a dorsal forest edge (Foggo et al., 2001, Ozanne et al., 2003).

There is a very distinct temptation to attribute the vertical stratification of arboreal fauna to a strict set of height/structural classes within the canopy of the forest. It was suggested by Richards (1952a) that a forest could have up to five distinct strata proceeding from the ground vegetation to the canopy crown. However, as was shown by Parker & Brown (2000) the separation of the forest canopy into a set of

clearly defined structural strata is not as easy as Richards suggested. Parker & Brown (2000) analysed past publications on structural canopy stratification and found that there were 10 differing definitions of structural canopy strata and how to measure them, these are listed below;

1. A synonym for height,
2. different life forms or age classes at different heights,
3. general variability in plant matter,
4. a continuous vertical distribution of foliar surfaces,
5. the vertical distribution of foliage,
6. a set of crown limits,
7. clumped leaf area with height,
8. species with different leaf heights,
9. species with different top heights, and
10. an index of vertical structure.

These definitions and measurements were then tested at a single temperate forest site to ascertain whether they were effective at defining if the canopy was stratified and if separate strata within the canopy structure could be identified. There were mixed results with a variety of answers produced from the differing approaches. Methods 3 did not state a required level of variability, method 6 had a subjective definition as it depended on what crown limits were chosen, 1, 5 and 10 were not applicable, 4 stated that there was no stratification within the canopy and 2, 7, 8 and 9 produced a positive result for the stratification of the canopy. The number of strata identified by the successful methodologies varied from 3 to 6 and method 10 produced a stratification index (SI) of 2.5 (using Ashton & Hall's (1992) index, although many other indices were used in the literature cited).

Parker & Brown (2000) go on to state that using a height (from the ground) as a meaningful proxy axis is not appropriate, as the ecological conditions within the canopy vary according to other gradients (temperature, light and other microclimatic factors to name but a few), which will show little height uniformity within a defined area of 1 ha for example. Therefore using height as the only determinant of stratification will obscure the actual factors that relate to the stratification of the canopy. This opinion is echoed by Bongers (2001) who states that it is hard to make generalisations on canopy structure as there are few standardised procedures used in past studies.

Bongers (2001) goes on to discuss the definition of the canopy itself and the myriad of definitions that there are. The author suggests five ways in which the canopy has been defined in the past, these are listed below;

- the collection of all crowns,
- the whole volume between and including the upper and lower crowns,
- the collection of crowns touching the canopy surface,
- the whole volume between and including the canopy surface crowns, and
- the whole above-ground forest volume.

Although Bongers (2001) describes the fifth definition as a radical view, the author uses this definition as he concludes it is best suited to analysing forest structure, because he believes forest structure can be apprehended as the physical structure and the spatial arrangement of all the above ground elements in the forest community. This definition is used by many other authors (see Whitmore, (1998), Basset et al., (2003) and Ozanne et al. (2003) for examples) as it links ground vegetation to the

upper most vegetation that interacts with the atmosphere. It is for this reason that this thesis will also define the canopy as all above ground vegetation.

Basset et al. (2003) group the main determinants of vertical stratification in arthropod communities into four categories: abiotic factors, forest physiognomy and tree architecture, resource availability, and arthropod behaviour. Basset et al (2003) also point out the inconsistency of the definition of 'stratified' arthropod assemblages. These authors follow the criteria set out by Intachat & Holloway (2000) who discriminate between (i) preferences in the vertical distribution of organisms from the ground to the over story (aggregated as opposed to uniform or random distribution), and (ii) strong clumping of these preferences in true 'strata' within the vertical column, resulting in clear boundaries and distinct arthropod assemblages. Basset et al (2003) considered the later as the strict definition of stratification in faunal communities.

With the difficulties in defining where one canopy stratum starts and finishes and even if there is indeed stratification in the structure of a forest at all, many researchers have simply investigated whether there are distinct differences between ground and arboreal faunal populations, with samples taken at ground level and then at a single or multiple pre determined height classes within the canopy. This avoids any biases in experimental design.

There is a wide variety of previous studies investigating the vertical stratification of faunal assemblages, which include both invertebrate and vertebrate species (see Kalko & Handley, (2001) (bats); and Winkler & Preleuthner (2001) (birds) for vertebrate examples. This review will concentrate on invertebrate studies, as this is the main focus of this thesis. A majority of the studies completed in relation to

vertical stratification of arthropods within the canopy have concentrated on the more easily identifiable taxa such as Coleoptera (see Davies et al. (1997), Stork et al. (2001), Chung (2004), Stork and Grimbacher (2006) and Grimbacher and Stork, (2007)) and Lepidoptera (see DeVries et al. (1997), Intachat and Holloway (2000), Schulze et al. (2001) and Brehm, (2007)), although other single taxa have been investigated such as; Diptera (Tanabe, 2002), Hymenoptera (Formicidae) (Nadkarni and Longino, 1990), Collembola (Rodgers and Kitching, 1998), Araneae (Sørensen, 2003) and Acari (Karasawa and Hijii, 2008) with a few mixed taxa studies (Nadkarni and Longino, 1990, Le Corff and Marquis, 1999, Basset et al., 2003, De Dijn, 2003, Ulyshen, 2011). However, as with entomology in general, multi taxon studies (and single taxon studies to a certain extent) are hampered by what Kitching (1993) calls the 'taxonomic impediment', which is the lack of qualified taxonomists to identify samples collected, which means that many species are only ever identified to a morphospecies level (mostly within a family or feeding guild grouping), rather than to a full taxonomic description. This is especially true of tropical species of which there is still relatively little known. However Hopkin (2007) also recognised a similar problem with the UK Collembola species, in fact two of the commonest UK Collembola this his book keys down to appear to be composites of ≥ 2 genetically isolated lines, Isotomurus palustris and Entomobrya nivalis (Shaw, 2011)

Schulze et al (2001) and Brehm (2007) investigated the vertical stratification of Lepidoptera within tropical rain forests. Schulze et al (2001) studied Lepidoptera, specifically fruit feeding nymphalids, a predominantly flower-visiting family of butterfly, and hawk (Sphingidea) and tiger (Arctiinae – subfamily of Arctiidae) moths in a Bornean rain forest. Brehm (2007) chose the species rich moth families of Arctiidae and Geometridae in a lowland rain forest in Costa Rica. Both of these studies did find vertical stratification among their chosen taxa, and both came to

similar conclusions of the drivers of that stratification. However there were certain differences between the two studies.

A notable difference between the two studies was the measures of α diversity. Both studies used Fishers α diversity index to measure the differences between understory and canopy assemblages yet Brehm (2007) showed that arctiid moths had a higher α diversity in the canopy with geometrid moths having a higher α diversity in the understory, where as Schulze et al. (2001) showed that α diversity in moths (including those from the subfamily Acrtiinea) did not differ between the two microhabitats, although richness and number of individuals of the subfamily Arctiinea was higher in the canopy. The reasons for this difference, especially that of the arctiidea family could be due to variations in collection method, differences in life history traits within the family, or differences in resource availability in the two forests.

The methods the two studies used differed in types of equipment used, Schulze et al (2001) used a gauze tower with a 15 W back light tube and collected the samples manually from 18:30 until 21:00 hr, where as Brehm (2007) used an automatic UV funnel-trap operated from dusk until dawn (ca. 18:30 – 05:30 hr). The extended sampling period used by Brehm (2007) could account for a greater diversity as well as reducing type one errors. The heights at which samples were taken in the canopy also differed as Brehm (2007) sampled at heights between 22 and 30 m where as Schulze et al (2001) used a standard height of 45 m. The sampling effort only differed slightly between the two studies (Schulze et al (2001) n = 42; Brehm (2007) n = 40).

The comparison of these two papers highlights one of the major problems that canopy science, as a discipline, has; that is the differing methods which are used to investigate the higher reaches of the canopy, and the site specific habitat conditions that each of the observed study site has. As was pointed out previously, the gradients of vertical stratification are not wholly determined by height within the canopy, instead a long list of abiotic and biotic factors all contribute to the availability of niche arthropod habitats within the canopy (Intachat and Holloway, 2000, Parker and Brown, 2000, Basset et al., 2003), and as yet there is no standardised method of sample collection for many taxa. Issues of methodology will be discussed further in Chapter 2. Both of these papers showed that there was vertical stratification of some kind within the Lepidoptera populations studied, although with some differences in approach and results.

One aspect of this study looks at the vertical stratification of Diptera within the forest strata, previous studies of this order are limited to well known family groups. An example of this is Tanabe (2002), who investigated the between forest variation of vertical stratification of drosophilid populations. Tanabe (2002) was not the first to study vertical stratification of this particular Dipteran family (see Toda (1992) and Beppu (1985) for a previous example of research in this area). It must be noted, however, that many of these studies were conducted in the Nakagawa Experimental Forest of Hokkaido University, Japan, so the results are limited to a very narrow band of habitat parameters. However all of these studies did show that there was clear stratification within the drosophilid assemblage at this study site. This would suggest that this family would show stratified assemblages at other sites.

So far the studies discussed have been concerned with flying arthropods; however there are also non-flying arthropods found in the canopy. Arthropods such as

Collembola, Acari, Formicidae, and many others are all found within the canopy. There have been numerous studies investigating the vertical stratification of these fauna. Here we will look specifically at the three aforementioned (sub) orders.

The non flying arthropods in the canopy are generally studied through the collection of suspended soil and litter, either in burghs where organic matter is deposited from falling leaves or in epiphyte/bryophyte mats. Epiphytes in the canopy pose another set of ecological questions about the changing microhabitat conditions within the canopy, as epiphytes have a significant effect on the microclimate in their immediate proximity. Stuntz et al (2002) showed that epiphytes significantly lower the temperature of their immediate surroundings and decrease water loss through evaporation by almost 20%. This then creates a niche environment for arthropods to live in and will influence distribution and community structure throughout the canopy. Furthermore epiphytes in the canopy of trees help to moderate extreme fluctuations in climate (Friberg, 1997), reducing their impact on the arthropod community. Therefore we must assume that the presents of epiphytes within the canopy structure will significantly influence the vertical stratification of the arthropods that dwell within them. It was also shown by Ellwood & Foster (2004) that the presence of large epiphytes within the canopy could, in some cases, double the abundance of arthropods within the canopy of a single tree.

Specific access and sampling methodology will be discussed in Chapter 2; however there is some controversy over how much epiphytes add to arthropod diversity. Yanoviak & Nadkarni (2003) showed that canopy fogging (a preferred method of assessing canopy arthropod diversity) only sampled some 30-33% of epiphyte dwelling arthropod, which would also account for Elwood & Foster's increased estimate of canopy arthropods due to epiphytes. Those arthropods of significantly

smaller body size (including many of the non flying species) were not collected during Yanoviak & Nadkarni's experiments in a cloud forest in Costa Rica. The authors believe that when taking into account the number of arthropods that were not sampled using the canopy fogging technique biodiversity in the canopy could be up to 70% higher than originally suggested. This particular study may not be wholly representative of canopy fogging as a methodology. There were certain site specific attributes that would have contributed to this result. The study was conducted in a cloud forest where there would be a large amount of epiphyte biomass found, so the result would be exaggerated compared to lowland forest which would have a substantially smaller epiphyte population.

Rodgers and Kitching (1998) collected samples of Collembola from epiphytes in an Australian sub-tropical rain forest. The authors split the canopy into three strata, ground, lower canopy and upper canopy, and then used a series of univariate, multivariate and randomisation techniques to analyse their results. Rodgers and Kitching (1998) looked specifically for dissimilarity in community composition between strata, and found that the ground and lower canopy were not significantly dissimilar but that the upper canopy was dissimilar. There were also canopy specialist species discovered within the samples, showing that there are purely arboreal Collembola species living within the canopy of sub-tropical rain forests in Australia.

Arboreal specialisation in non flying arthropods has been noted by many authors (see Rodgers and Kitching (1998), Walters et al. (1998), Yoshida and Hijii (2005), Fagan et al. (2006), Shaw et al. (2007) and Yoshida and Hijii (2011) as examples), with some species migrating from the ground soil to canopy suspended soil/litter, bark and leaves seasonally (Itoh, 1991, Yoshida and Hijii, 2005). Nadkarni and Longino

(1990) reported vertical stratification and canopy specialism within two genera of ants in a Costa Rican cloud forest. The results of their experiment showed that even within the genera of *Stenamma* and *Pheidole* canopy specialism and vertical stratification was apparent. On further investigation no morphological difference between the ground and canopy species could be found which would indicate arboreal adaptation.

However adaptation to arboreal conditions can be seen in a study by Yoshida and Hijii (2011) who investigated the colonisation of arboreal litter by macroarthropods. In it the authors show that canopy specialists, like the Oribatida, will maintain a constant presence within decomposing arboreal litter. However Collembola, Gamasida and Prostigmata will arrive much later when the decomposition process has reaches a certain point. The authors attribute this to the fact that arboreal litter decomposes slower than at the forest floor. Slower decomposition rates would prove to be unfavourable to as nutrients would be released into the system slower and there would be less available food resources; therefore, specialised species, such as the Oribatida, would be able to survive in less than favourable conditions.

The studies cited here have shown that there is stratification of arthropod communities within the vertical gradient of tropical, sub-tropical and temperate forest systems. Further to this there is also a certain degree of canopy specialisation within the arthropod community, with species showing either a preference for the canopy, migrating to the canopy seasonally, or a complete arboreal existence. The literature also points towards the importance of epiphytes within the canopy, acting as islands of diversity, offering niche habitats and protection from extreme climatic events.

1.4 Edge Effects

Ries et al (2004) surmised that edges between habitat patches were often ecologically distinct from patch interiors, and that understanding how ecological patterns changed near the edges was key to understanding landscape-level dynamics such as the impacts of habitat fragmentation. Edge effects are defined in conservation biology as the creation of a distinct edge between previously undisturbed forest and a deforested clearing (Marsh, 2003). This is different from the ecological term that defines a natural edge between two distinct habitats (Marsh, 2003, Ries et al., 2004), instead we have a situation were there is an edge between a habitat and a non habitat or a habitat of much lower quality. One process that leads to increased influence of edge effects is that of forest fragmentation, as it leads to an increase in the amount of forest edge (Chiarello, 2003), because as forest patches decrease in size and become more irregularly shaped, the edge/interior ratio becomes more pronounced (Didham, 1997, Ries et al., 2004). The edge of a forest fragment can have many influences on the forest ecosystem. Edge effects can alter species distributions and physical gradients, along with many other ecosystem processes (Didham, 1997, Turner, 1996, Ries et al., 2004). Ries et al (2004) suggested four underlying mechanisms of edge effects based on empirical data. These mechanisms were;

- ecological flow - movement of light, heat, moisture and wind from one patch to another),
- access – ability of species to utilise resources on either side of the edge,
- resource mapping - abiotic gradient changes due to creation of an edge, and

- species interactions – interaction in which one species benefits from another (predation, parasitism, herbivory).

The main abiotic factors propelling edge effects are the changes in microclimate at the edge, including reduced humidity, increased light penetration, and higher temperature variability (Bierregaard et al., 1992, Laurance et al., 2002). Microclimate changes can also affect the trees already present at the newly formed edge. Because of the increased wind-throw, reduced humidity and increases in ambient temperature, tree mortality and tree damage can increase. This then leads to the appearance of canopy gaps, which will in turn increase the amount of secondary succession that protrudes into the forest core (Laurance et al., 2002, Marsh, 2003). Furthermore, observations in South America have revealed that as well as tree mortality being high at the edge of fragmented forests, leaf decomposition is slowed, which may lead to difficulties in germination of new seeds and reduce preferential niche habitat for litter and soil dwelling arthropods (Laurance et al., 2002). In terms of vegetation and a majority of vertebrate species, these abiotic effects can penetrate up to 60 m into the fragment, and therefore the size and shape of the fragment can increased or decrease these effects (Kapos, 1989, Turner, 1996, Laurance et al., 2002, Hill and Curran, 2003). However, Didham (1997) believed that edge effects for invertebrates might penetrate up to 100 m from the edge, and in a later paper by Ewers and Didham (2006) suggest that by using non linear regression models, edge effects can be shown to straddle the edge of the forest penetrating 100's of meters both into the forest and the adjacent habitat (eg. grassland).

Didham (1997) summarised invertebrate responses to fragmentation and edge effects. He surmises that invertebrate abundance will increase towards the edge of the forest due to the replacement of natural forest populations with invasive

(generalist) edge species. However there are often ecological differences between the edges of continuous forest and that of smaller, sometimes isolated, forest fragments. Other authors are less general in their opinion, characterising different responses by different orders and species based on their habitat and life history needs (Foggo et al., 2001, Deans et al., 2005, Schowalter et al., 2005, Ostman et al., 2009). What is accepted by a majority of authors is that there should be some response by invertebrates to the presents of edge habitat, as the microclimatic variations and subsequent habitat gradient produced by edge proximity directly influences arthropod niche habitat.

However there are some cases where no detected response was found. Shaw et al (2007) studied the edge effects of a coniferous plantation on arboreal Collembola. Sixty statistical tests were conducted on the data set, of which only four showed significant edge effects in the Collembola, none of which fitted the exponential model (suggested by Ewers and Didham (2006)). By contrast in the same dataset micro-meteorological data, temperature and humidity (collected at 1.5 m above the forest floor), all showed significant edge effects. There was therefore no correlation between the two environmental factors and Collembola community patterns. This fits with one of Ries et al (2004) underlying mechanisms, that of resource mapping. Arboreal Collembola are relatively less mobile than other arboreal arthropods, therefore would react to variations of niche habitat (resources availability). Therefore where you have a biological system with near-perfect homogeneous structure (equally distributed trees, reduced understory vegetation) one would assume that Collembolan resources are equally distributed throughout the system irrespective of proximity to edge and would show no discernable edge effects, though with substantial and purely stochastic variation from tree to tree.

Much like vertical stratification, the literature surrounding edge effect seems to be quite site or study specific, with the presence, magnitude and penetration of the effect varying from study to study and methodology to methodology. Of all the studies discussed here, Ewers and Didham (2006) seem to have the most comprehensive and statistically valid method for detecting edge effects in invertebrates. This study uses a tool kit of linear and non linear regression models to investigate the abundance of various orders of arthropods across a forest boundary. The authors believe that if the edge can affect the abundance of arthropods within the boundary of the forest then there should be an opposite relationship within the adjacent habitat. This follows closely with Ries et al. (2004), who described the flow of energy across the boundary of habitats.

Although it may not be possible to collect data on the scale of Ewers and Didham (2006), using the regression models they have suggested in their paper would be an interesting investigation. Therefore this thesis will use the models proposed by these authors to investigate edge effects.

The literature above has shown that there are variable responses to edge effects by different species of arthropods. Whereas Didham (1997) stated quite clearly that arthropod abundance should increase at the edge of a forest habitat, others have suggested other dynamics may be present. Whereas the overall abundance may increase, it is more than likely that the community will be dominated by a few more generalist or mobile species rather than being as diverse as a forest interior. So in terms of the present study the predicted result would follow that abundance may increase at the edge of a forest but the diversity will be likely to decrease.

1.5 Savannah Burning

One element of this study is to investigate the effects of burning savannah grassland on the abundance and richness of Diptera and Collembola within the adjacent forest edge. The practise of burning savannah in Africa is a management tool which has been used by indigenous peoples for millennia in many grassland areas of Sub Saharan Africa (Oluwole et al., 2008). The argument for burning savannah grasslands during the dry season (not limited to Sub Saharan Africa) include habitat conversion (Fujisaka et al., 1996), hunting, agricultural clearance, pest control, removal of dry vegetation, promotion of agricultural activity (increasing potassium and phosphorus levels within the soil), and hunting (Bucini and Lambin, 2002).

Policy concerning burning regimes in West Africa has been distinctly anti-fire since roughly the middle of the 20th century. This is due to several long term experiments conducted by colonial governments (eg Stebbing (1938), Aubréville (1938)), which demonstrated that savannah burning had an adverse effect on forests. As a result of these burning experiments modern post-colonial government policy usually takes the form of a hierarchical system where fire exclusion is the ultimate management objective, fires set early in the dry season are only acceptable under specific conditions, and late fires are seriously discouraged and often illegal, based on the findings of these previous experiments (Laris and Wardell, 2006). As it is believed that anthropogenic fire has been an element of habitat management for 400,000 years in Africa (Bird and Cali, 1998), the imposing of an effective ban on this cultural practise has always been a source of conflict and contention between the rural population and the Forest Services. Despite a century of education and awareness

campaigns to promote anti-fire legislation fires have continued to be set, which shows that this strategy has wholly failed to produce a significant change in indigenous burning practises or a reduction of the annual area burned (Laris and Wardell, 2006).

So is burning a bad thing, and why would rural populations continue to practise burning if there were significant adverse effects? Laris and Wardell (2006) concluded that the original colonial experiments were biased due to the fact that colonial governments valued forest more than grassland, due to the greater economic contribution that they made. The current literature evaluates the effects of fire from two view points; the first from the benefit to the habitat in terms of agricultural production; and second the effects that fire has on the habitat from an ecological perspective. There is little literature that investigates the specific effect of fire on invertebrates within tropical forest edge habitats, although Swengel (2001) and Uys et al. (2006) have reviewed and summarised insect response to fire in temperate and tropical savannah habitats respectively.

Bucini and Lambin (2002) used remote sensing data to investigate land cover change due to early and late burning in the southwest of the Central African Republic. Data were analysed using multivariate regression models from maps of land cover change derived from remote sensed data, maps of burnt areas and a detailed map of ecotypes. Laris (2002) showed that in areas such as Mali, indigenous communities would burn some areas as soon as they were dry enough in order to separate the land into burned and unburned patches to control later anthropogenic burning and prevent late season accidental wildfire. Therefore Bucini and Lambin (2002) investigated the impact of these differing regimes on land cover-change, assessing the impact of early and late season fires on different ecotypes. The results from the study showed that in

adjacent dense forest, burning was strongly associated with land cover-change, however savannahs were largely unaffected by early burning with little land cover-change. The study confirmed that early burning fragmented the landscape and prevented damage caused by late burning, which was itself confirmed by the prevalence of late fires in areas where there were no human settlements present. The study also showed that there was an increase of grassy vegetation in some areas of very early burning, and that the dense semi-humid forests were significantly affected by high levels of burning on their peripheries due to land use. The conclusions of this study note that burning maintains and in some cases enhances the savannah grassland but can also adversely affect dense forest which has few fire resistant species. However if savannah areas are left unburnt then later dry season wildfires will have a greater impact on both the savannah and subsequently the adjacent dense semi-humid forest.

Some of the adverse affects of accidental fire in semi-humid forests were investigated by Badejo (1994) who studied its effects on soil mite densities in a Nigerian forest subjected to an accidental fire. The results of this investigation showed that although there was some recovery by the mites, some genera were lost, others never recovered to their pre burn status (within six months), and some species, in particular juvenile cryptostigmatid showed a higher density in burnt plots. The author attributes the changes in density to differences in feeding requirements, phenological patterns and life history tactics of the mites, and suggested that the fire increased the reproductive activities of the cryptostigmatid mites. As with many arthropods, mites can be highly affected by changes in microclimate, due to their small body size and, in some cases, niche habitat preferences. Therefore factors such as increased heat at the soil horizon, influx of nutrients and loss of above ground

vegetation create a change in both microclimate and microhabitat which will, in turn, affect small bodied organisms living in and around the soil horizon.

Uys et al. (2006) summarised insect responses to savannah burning from numerous sources and concluded that strong flying taxa decreased in the area immediately after a fire either through dispersal or mortality, soil invertebrates were only weakly affected by fire since soil temperatures (below the soil surface) were relatively low, and that mean body size of invertebrates decreased, also because of the greater ability of larger bodied invertebrates to disperse. The authors went on to say that litter dwelling arthropods had limited dispersal capabilities and were more likely to decline in abundance. One must note that Uys et al. (2006) quotes much of this information from Tainton and Mentis (1984) which therefore did not take into account later studies of soil invertebrates such as Badejo (1994).

Anthropogenic burning of savannah grassland in West Africa is a controversial issue and the results of studies can often be influenced by the authors' particular opinion on the practise. However what is clear is that it is a practise that is not going to be eradicated in the near future. Therefore one must assume that it will continue and that the effects need to be clearly studied in a non emotive fashion in order to ascertain the impacts that it has on tropical forest biodiversity.

1.6 Conclusions and research questions

Diptera and Collembola have been shown to be good indicators of habitat heterogeneity, as they are affected by both abiotic and biotic factors. The literature has also shown that forest canopies are important to the overall biodiversity of the

forest habitat as they contain a diversity of habitats increasing the available niches that arthropods rely on for survival. The habitat niches themselves are affected by biotic and abiotic parameters as proximity to the edge will create changes in microhabitat and microenvironment, hence generating a variety of new habitat niches for arthropods.

This review of spatial and temporal patterns in invertebrate abundance has shown that there are a great many factors that contribute to arthropod community structure. These factors include seasonal macro and micro climate, resource availability, habitat quality and anthropogenic pressure. This thesis will address these elements both individually and in combination in order to achieve a greater understanding of tropical forest ecological dynamics. To that end three research questions will be asked.

1.) How does the pattern of abundance and richness of Diptera and Collembola change through the vertical column, and how does the change in season from dry to wet affect that pattern?
2.) What effect is there on the pattern of abundance and richness of Diptera and Collembola due to burning the adjacent savannah, and what part does the change in seasons play in that pattern shift?
3.) What are the underlying edge effects within the habitat, how do they affect the community structure of Diptera and Collembola, and to what extent do the environmental conditions contribute to that effect?

These three questions are focused on the physical structure of the forest addressing two physical gradients, that of height within the canopy and distance from the edge (with an edge manipulation experiment), and one environmental gradient, that of

seasonal change and the influence of environmental conditions. The above literature showed these factors to be closely linked, therefore this thesis is also an opportunity to combine these factors and draw a picture of the whole habitat rather than just a single element. It will also be possible to focus analysis at a finer scale than order or suborder and show how these varying structural and environmental factors affect organisms at the family level.

Chapter 2: Methods Introduction

2.1 Canopy Access Techniques

Sutton (2001) tells us that the scientists of the nineteenth century used climbers from the local human population to scale the canopy and collect specimen's mostly for the purposes of identification. These local climbers were more used to climbing trees in the pursuit of forest products such as honey and fruit. However Sutton (2001) points out that the need for replication and manipulative experimentation showed that the use of local climbers was in fact inadequate, as the researchers were limited to certain trees where suitable vines and lower storey trees were available for purchase by the climbers. Observations by these early pioneers were mostly limited to ground based recordings, probably using equipment such as binoculars and telescopes. However, their use did provide good information (and still does) on larger more gregarious species of birds, mammals, reptiles and larger arthropods.

The Second World War was a major interruption for most ecologically based scientific investigation. However, it did provide the basic building blocks for some of the materials that were later used in canopy access (high strength, light weight metals and polymer materials) (Sutton, 2001). The next innovation came in the 1950's with the first use of towers to access the higher reaches of the canopy. This method of research is one that has continued into the 21st century with a system of canopy towers and cranes installed all over the world (see the IBISCA Project as a working example (Leponce and Basset, 2009)).

The early 1970's saw the use of canopy fogging to 'knockdown' arthropods from the canopy onto trays and sheets at the bottom of the tree, and towards the end of the 1970's researchers started to borrow climbing techniques from caving and mountaineering (Sutton, 2001). The introduction of a wide variety of canopy access techniques has allowed canopy science to develop, with the last three decades showing an increased pace of investigations, and a dramatically faster rate of publication.

Quite often the limiting factor of the type of research that can be conducted in the canopy of forests is the type of canopy access methodology that is available to the researcher. The largest factor in deciding which access method to use is the cost and availability of equipment and resources. Barker and Sutton (1997) assessed canopy access methodology. This paper followed a survey compiled by Nadkarni and Parker (1994), who showed that canopy access was the greatest obstacle to the advancement of canopy science.

In this review, Barker and Sutton (1997) divide canopy access methods into low and hi-tech categories. Low-tech methods are generally those that require simpler equipment that can normally be carried by one or two persons within the forest, where as the hi-tech methods need larger teams, logistic organisation and qualified personal to install and operate them. The low tech canopy access methods include all methods that can collect information and samples from the forest floor without personal having to leave the relative safety of the ground, as well as those that require relatively small amounts of equipment for personnel to physically access the canopy. Methods such as these are relatively cheap and most need little or no specialised equipment and training.

- Slingshots and firearms for collecting branch samples.
- Pole pruners and long handled nets.
- Tree felling.
- Binoculars, radio tracking and photography.
- Equipment raised into the canopy; cameras, nets, insect foggers and micro-meteorology sensors.
- Tree climbers; local personnel often with no equipment or sometimes with just a foot loop.
- Free climbing (using ropes), or bole climbing (ladders, spiked leg irons and 'tree grippers').

The hi-tech methodologies described by the authors are ones that have been developed, in some cases, since the 1950's (see Sutton (2001)). These hi-tech methods can allow for collaborate research, which is often needed to keep the projects economically viable. Barker and Sutton (1997) do however state that these hi-tech methods are impractical for some canopy research because of the high establishment and operating costs. The authors list them as;

- Towers
- Cranes
- Arial walkways and platforms
- Scaffolding
- Hydraulic lifts
- Tower ladders
- Booms
- Cable cars
- Hot air balloons

- Canopy rafts
- Ultra light aircraft

A good example of collaborative research using a mixture of low-tech and hi-tech access methods is the IBISCA project, which has installed towers and cranes and deployed canopy rafts and balloons in Central America, the South Pacific, France and Australia (Basset et al., 2007). The project aims to study beta-diversity, vertical stratification and seasonality of a wide variety of arthropod groups, along with their ecology and relationships with forest processes and the impact of forest disturbance (see Springate and Basset (2004), Pennisi (2005), Roisin et al. (2006) and Medinaero et al. (2007) for examples of outputs from this project). The IBISCA Project has succeeded in bringing together entomologists from all over the world and combines their expertise in order to fulfil its research objectives. Because of the scale of this thesis the installation of such hi-tech canopy access methods would be wholly inappropriate. Therefore we must consider the low-tech alternatives, such as rope access.

Canopy researchers started to use rope climbing techniques in the early seventies (Denison et al., 1972, Perry, 1978, Perry and Williams, 1981, Risley, 1984, Barker and Sutton, 1997, Sutton, 2001). The technique was first borrowed from caving (spelunking/potholing) and rock climbing and then later from the arborealist (tree surgery) industry, and has developed over the years into two distinct categories of techniques; Single Rope Technique (SRT) and Double Rope Technique (DRT).

Denison et al (1972) first developed the rope access technique to avoid damage to the tree that they were sampling, while Perry (1978) was really the first to fully utilise expertise from rock climbing and caving to access the canopy. A major concern that

was voiced about this particular technique was that it only offered a narrow vertical column for researchers to operate within. However Perry & Williams (1981) provided a method that could be utilised to access the entire canopy, using a central platform and then a system of connecting aerial ropes suspended from surrounding trees to access the outer reaches of a tree's canopy.

The problem of moving all this equipment to survey sites still impeded some researchers. Risley (1984) developed a method for accessing trees in remote areas, using equipment that could be transported through the forest by one or two persons. The method the author used resembles very closely the modern ways of accessing tree's using either SRT or DRT. Risley (1984) fashioned a seat harness, very similar to the modern commercially available equivalent, from 1.5 m of 70 mm diameter nylon webbing, the author then attached a Gibbs® ascender at the front via a karabiner, this then attached to a vest made from a cinch strap with attached nylon webbing, creating a full body harness. The Gibbs® ascender prevented uncontrolled decent and allowed the climber to remain stationary in the canopy without further physical exertion. Movement vertically up the rope was achieved using a pair of hand ascenders with foot loops attached. The modern equivalent to Risley's (1984) climbing equipment is called Personal Protective Equipment (PPE), designed to protect against 'imminent mortal danger' and is subject to the Lifting Operations and Lifting Equipment Regulations 1988 (LOLER), as climbing equipment is classified as lifting equipment (Aldred and Pike, 2008). The modern equipment consists of a seat harness, attached to a chest harness through a chest ascender (a Petzl CROLL®, fig, 2.1c), vertical movement is achieved through hand ascenders and foot loops (Petzl ACENTION® fig 2.1b and FOOTPRO® fig 2.1e), desent from the canopy is done using pulleys (a Pezl GREGRE®, I'D®, or STOP® fig 2.1d), see fig 2.1 (a) below for correct set up.

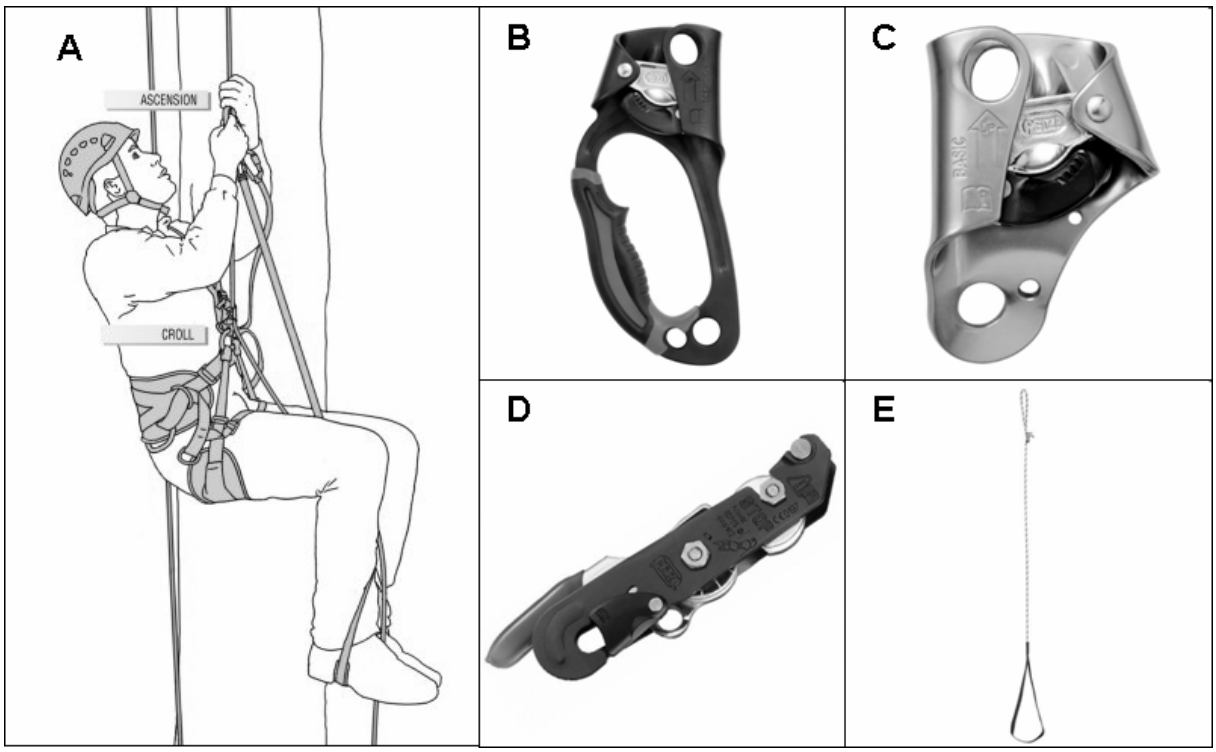


Fig 2.1. A.) diagram of single rope technique taken from http://www.rescueresponse.com. B.) Petzl hand ascender, C.) Petzl chest ascender, D.) Petzl rope decender, and E.) Petzl foot loop. All Petzl images taken from http://www.petzl.com

The most obvious disadvantage that the use of this technique poses is that researchers need to be fully trained in order to use this access method, as it could possibly result in serious injury or death if the proper protocols are not observed (Risley, 1984, Barker and Sutton, 1997, Sutton, 2001, Aldred and Pike, 2008). Other less critical problems with this access technique are mostly concerned with 'rigging' the tree. Many studies that have used SRT or DRT in the past have used a crossbow and fishing line shot into the tree, and then used the fishing line to pull the main climbing rope(s) into the tree. However the process can take a long time, finding suitable trees with large branches in the upper canopy, and then the actual placement of the line over that branch can take between 15 minutes and 3 days (pers. obs.). There are also alternatives to the use of crossbows to fire the fishing line (or similar) over appropriate branches. This example comes directly from the arborealist industry.

Most tree surgeons use large sling shots (for example the Jameson Bigshot®) to launch a special weighted 'throwline' into the tree (Aldred (pers comm.) recommends this as when travelling overseas it is much easier to get this through customs than a crossbow). It may not reduce the amount of time to 'rig' the tree but it is a lot less dangerous than using a crossbow.

2.2 Sample Collection Techniques

Because of the differing methods used to sample tree crowns finding definitive patterns in arthropod distribution within the structure of the canopy from the literature is difficult. The methodologies which have been used within the literature analysed include; canopy fogging (see Cruze-Angon et al. (2009), Fannes et al. (2008) and Bos et al. (2007) for recent examples), baited traps (including light traps) (see Bourguignon et al. (2009), Jansen et al. (2009) and Stelinski & Rogers, (2008) for recent examples), flight intercept traps (FIT, including Malaise and Composite intercept traps) (see Basset (1988), Hill and Cermak (1997), Wells and Decker (2006) and Campbell and Hanula (2007) for examples), colour traps (including pan traps) (see Toler et al. (2005) and Laubertie et al. (2006) for reviews of methods), arboreal pitfall traps (Weiss, 1995), and various canopy access methodology has been used including; rope techniques (both single and double), areal walkways, cranes and towers, and canopy balloons and platforms (see Sutton (2001) and Lowman (2009) for a history and review of these methods). There are also certain methodologies used to sample arthropods that reside in suspended soil and litter within the canopy, the collection methodology is mostly standardised for these taxa; however the extraction techniques do differ between studies and taxa (see Winchester (2002), Winchester and Behan-Pelletier (2003) and Yoshida and Hijii (2008) for examples of various extraction techniques).

The studies that have used canopy fogging offer only a snap shot of distribution from a particular time of day with a particular set of climatic conditions. An example of this can be taken from Stork et al (2001) who investigated the lateral distribution of coleoptera in oak trees (Richmond Park, UK). Trays were placed at various positions under the tree to represent differing distances from the trunk and compass bearings. The results indicated that there are patterns of beetle distribution through the oak trees sampled. The authors found that there are some species of beetle that are more associated with the trunk, some species that are more associated with the outer regions of the tree crown, some species prefer certain compass sections of the tree, and that the distribution pattern of some species changes throughout the year. However the authors do concede that there are many variables that may affect the spatial distribution of the beetles within the canopy. Vegetation density, presents of large fungal masses, changes in surrounding vegetation are quoted as being probable causes for the spatial distribution. More interestingly the time of day was also mentioned, as there are many more tourist species present during the evening that are not found at mid day.

An importance of collection method is also highlighted by Chung (2004), who also studied vertical stratification in beetle communities. Chung (2004) used flight intercept traps suspended at different levels to ascertain spatial variance in an arboretum in Borneo. Samples were taken from ground level, 6 and 12 m intervals with species identified to family and morphospecies taxonomic levels. Chung (2004) points out that the study shows a significantly higher biodiversity of beetles at ground level than at the upper sampling points, mainly due to the presents of dung beetles at ground level and not within the canopy structure, and further points out that the use of fogging techniques would underestimate the population of beetles at

ground level. However; there were serious limitations in this study as there were too few sample repeats and only a small number of data points analysed, and that the arboretum forest structure did not resemble that of a mature dipterocarp forest (arboretum canopy height ~50 – 60 m lower than that of a mature lowland dipterocarp rain forest) to which the author was alluding to.

Yanoviak et al. (2003) also point out that canopy fogging in tropical forests is not efficient at sampling arthropod species within epiphytes. In their paper they conducted pre and post fogging sampling in a rainforest in Costa Rica and found that canopy fogging only sampled 30-33 % of the arthropod richness within epiphytes. They believed that a majority of the arthropods were caught in the epiphyte mat and failed to be collected by trays placed under the tree, with the majority of the arthropod species that were collected having a larger body size and mass. This particular study may not be wholly representative of canopy fogging as a methodology. There were certain site specific attributes that would have aided this result. The study was conducted in a cloud forest where there would be a large amount of epiphytes found, so the result would be exaggerated compared to lowland forest which would have a substantially smaller epiphyte population.

Although most of the previous comments here have been negative towards canopy fogging, there are occasions where the results have been very good (see Shaw et al. (2007) for example). It is really a case of choosing a sample collection methodology that fits the project, will most suit the type of research that is being completed and most importantly fit the habitat that is being studied. As the field site chosen for this study is not cloud forest and should have a relatively low epiphyte population (no large arboreal ferns for example) then canopy fogging is a possibility, however

collecting samples from discrete heights within the canopy may prove to be problematic using this methodology.

The sampling of flying arthropods has in the past been conducted using flight intercept traps (see Chung (2004), above, for an example of this survey method) and malaise traps. These two distinct sampling methodologies use the in-flight behaviour of arthropods to aid their collection. Insects such as Diptera, Hymenoptera and Lepidoptera tend to fly vertically up when coming across a vertical surface, hence the malaise trap is the most successful at trapping these species as its collecting jar is at the top of the trap. Whereas arthropods such as Coleoptera will close their wings and drop when flying into a vertical surface, hence the success of flight intercept traps at sampling these species as its collection tray/jar is positioned at the bottom of the trap. However if the researcher wanted to sample multiple species with both in-flight behaviour traits, they would have to deploy both traps. Therefore Basset (1988) proposed a trap that would combine the qualities of both trap types in one. The design was basically a malaise trap with a fin style intercept trap suspended directly below it, which was then hoisted into the canopy. This original design has now been modified and has become a fully integrated composite intercept trap (as used by Campbell and Hanula (2007)). The use of this trap type increases the volume and diversity of arthropods that are collected at any one site, and can aid multi taxa sampling research (see figure 2.4).

As stated earlier in this chapter, in order to sample a large proportion of possible collembolan habitat it is important to take into consideration the soil and leaf litter surrounding and contained within (suspended soil/litter) the tree. Collembolan studies involving investigation of the soil have been conducted for a very long time, however, there are three main methods for extracting the organisms from the soil

once it has been collected, these are; Tullgren Funnels, hand sorting and Winkler bags.

Tullgren funnels (or Berlese funnels) were invented by Berlese in 1895 and then adapted by Tullgren in 1918 (Macfadyen, 1953) and have been used, in various designs, since then to extract arthropods from soil. The design of the extractor is based around the fact that as the soil is heated and dried from above the arthropods will move away from the dry heat to where the soil moisture is retained. This means that the arthropods are effectively pushed vertically down away from the heat/light source and out of the bottom of the sample which is suspended above a funnel. The arthropods are then collected in a tube underneath the funnel. The original Berlese funnel only used a heat source however the later Tullgren design incorporated a light bulb to increase the speed of the process.

The Winkler bag/extractor was invented by Moczarski in 1907 and put on the market by the Winkler and Wagner Company where it got its present name (Krell et al., 2005). The leaf litter/soil are placed in a mesh sack and suspended within a closed sack of cloth, with an alcohol containing bottle suspended at the bottom of the sack. As with the Tullgren funnel the organisms move through the substratum as the material dries and fall out the bottom of the mesh bag and into the bottle at the bottom of the sack. This method is much simpler than the Tullgren/Berlese funnel as it does not require an electrical source to power the extraction and is thus better suited to use in more remote locations.

Each of the three methodologies has their advantages and disadvantages and therefore the best methods must be chosen to suit the particular study being conducted. Smith et al. (2008b) compared the three methodologies in extracting

macrofauna from soil cores taken from arable systems in the UK. Smith et al. took nine samples per method from four vegetation types; the hand sorted samples were sorted for 20 minutes, and the Tullgren funnel and Winkler bag samples were extracted over a period of seven days. The results of the study showed that after Bonferroni adjustments had been made there was no significant difference in the abundance of macrofauna extracted between all three methodologies. Although this paper does not study Collembola specifically it does state that this was due to the large numbers of individuals extracted by all methods. There may of cause be differences in tropical and temperate Collembola assemblages which will have to be taken into account during the study.

Due to the remote area in which this study is taking place, the lack of continuous power and only a single researcher available to conduct the sample collection, a low technology, low man power solution is needed to extract arthropods from the soil samples. Therefore Winkler bags were used as they do not require an external power source for extraction to take place, and as there will only be one researcher responsible for their collection it is unlikely that there will be time enough in the field to extract organisms by hand.

Another habitat which Collembola are known to inhabit is the bark of trees; therefore it is also necessary to investigate this within the study. Methods to collect samples from this habitat include insecticide knockdown, arboreal pitfall traps and vacuum sampling. When deciding which of these methods is best suited to this particular thesis it is important to take into consideration the areas within the tree which are to be sampled. This is particularly important as the researcher will be suspended for much of the time from a rope up to 30 m above the ground, therefore equipment must be easy to either install or operate at this height.

Kitching et al. (2005) described the use of insecticide knockdown for bark dwelling arthropods in their methods manual for the Earthwatch Institute. In it the authors recommend that a modified collecting hoop (a collecting hoop used in large scale knockdown methodology, with roughly 1/3 of the outer rim removed) is firmly attached to the trunk of the tree with a collecting bottle suspended under the opening at the bottom of the net. A household insecticide aerosol is then sprayed over an area of 1 x 0.5 m directly above the collecting hoop at a distance of 1 m from the bark. Then over the next 30 minutes the bark is carefully brushed to remove all the arthropods from the bark and into the collecting bottle. The results published by Kitching et al. do show that a high abundance of Collembola are sampled, however the use of this methods may prove to be to cumbersome when 30 m or more above the forest floor, and would greatly increase the time spent in the canopy for the researcher. Therefore this method, although effective for sampling Collembola, would not be appropriate for this study.

Arboreal pitfall traps come in various shapes and sizes and are generally modified by the researcher to his or her specific project needs. Two examples of designs can be seen in Weiss (1995) and Kaspari (2000). Weiss's design attaches directly on to the trunk of the tree and is designed specifically for sampling Araneae, although other taxa would also be sampled. Kaspari has a simpler design that doesn't even need canopy access in order to set it up. A small line in launched over a branch with a small handheld catapult; the line is then used to pull a small pice of leather (10 x 30 cm) with a slit at one end in which a test tube containing a killing agent is placed. The leather strip is secured at both ends by guy lines and the leather strap itself is suspended over the branch with the test tube to one side. Arthropods are then caught in the test tube as they walk over the leather strap. Both methods have their

advantages in sampling, although the simpler design of Kaspari (2000) may suit this thesis slightly better, as it can be modified and easily placed in the canopy.

Modified vacuums have been used extensively in the collection of arthropods, although generally they are used to sample ground based vegetation rather and arboreal habitats. However there are now some researchers attempting to move this methodology into the trees. In a paper by Bussler & Muller (2009) a modified vacuum cleaner was used to sample dead wood inhabiting beetles. The methodology seemed to work in this instance and this species of beetle was successfully sampled. It is therefore likely that collecting directly from the bark of living trees is also possible. Although a smaller vacuum model than the one used by Bussler and Muller would be vital so as to carry it into the canopy.

From the sampling methods discussed above it is necessary to choose the right methods for both the taxa to be studied and the site in which it is to be sampled. As many of the samples will be taken high up in the canopy of the forest it is essential that the equipment is light weight and practical for arboreal sampling. Therefore from the methods above the techniques chosen were Composite intercept traps, soil samples (extracted with Winkler bags) and a form of vacuum sampling.

2.3 Thesis Methodology

2.3.1 Site selection

This study was conducted in the Gashaka Gumti National Park (06º 55' - 08 º 13' N and 11º 13' - 12º 11' E), situated in North Eastern Nigeria close to the Cameroonian border and north of the Mambilla plateau. The park covers an area of 6600 km^2 and is the largest National Park in Nigeria. The park consists of numerous habitat types including savannah grassland, forests and high mountain plateaus. The Park was created in 1991 by federal decree combining the existing areas of the Gashaka Game Reserve and the Gumti Game Reserve. The southern sector (Gashaka) varies in altitude from 300 m to 2,419 m and consists of a mixed rugged terrain. The area's highest point (Chappal Waddi, Nigeria's highest mountain) is an important catchment area and supplies water to numerous rivers throughout the region (Sommer et al., 2004). The study area was situated at the Kwano Research Centre (583 m; 07°19' N, 11°35' E), an abandoned settlement roughly 10.5 km east of the village of Gashaka. The elevation rises to 1200 m (asl) roughly 3.5 km to the east of the research centre, and this steep incline holds a majority of the Kwano forest which consists of gallery and riverine forest habitats and is largely intact primary forest. To the west and south of the research centre the habitat becomes a matrix of Guinea savannah and fragmented forest habitat.

The climate of the Kwano forest is heavily influenced by the West African monsoon, which produces a single dry season from roughly mid October to mid March where rain fall is < 2 mm, maximum temperature is 36º C and average humidity (humidity value measured at 1800 hrs) is 50 RH% (mean values per day), to a single wet season

which peaks in September where mean daily rainfall is 14.11 mm, maximum temperature is 30 - 31 º C, and average humidity 92 %RH (taken at 1900hrs daily) (environmental data taken at the Kwano weather station 2001-2009).

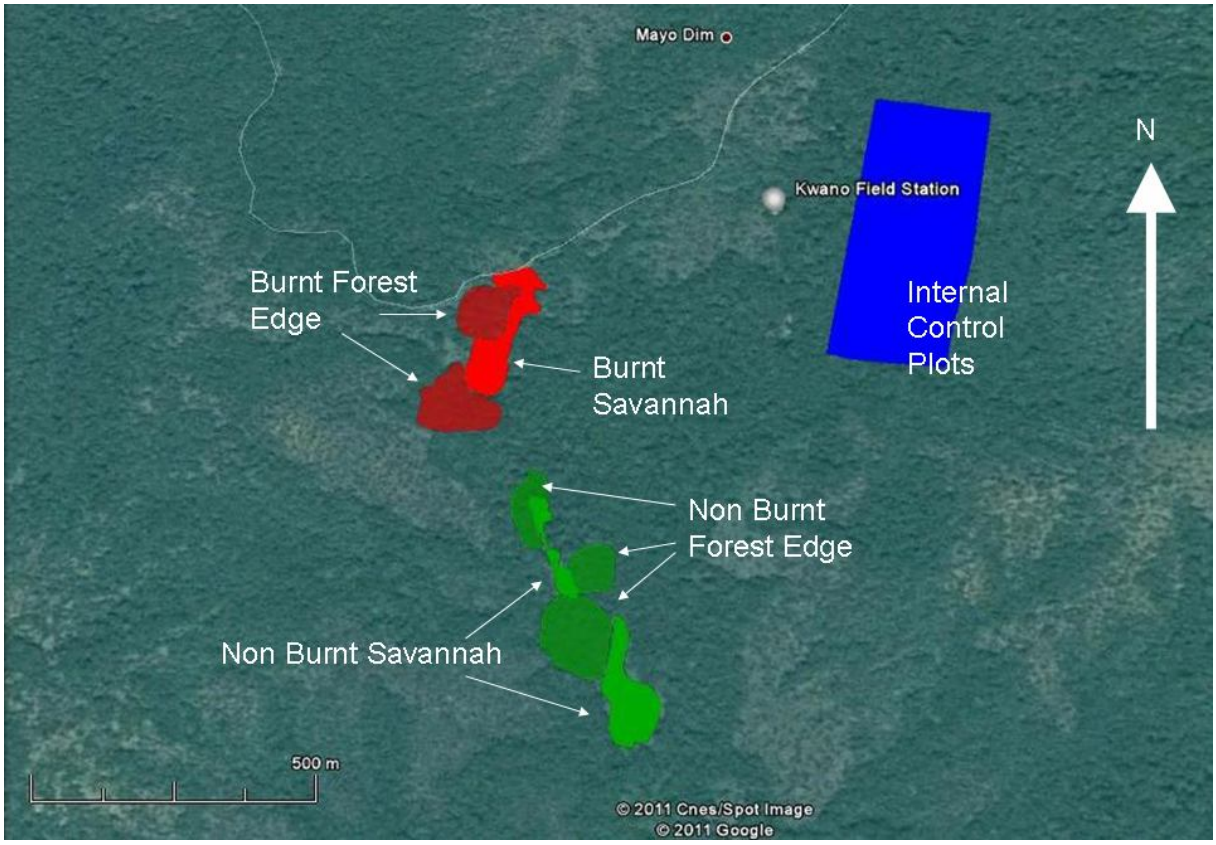


Fig 2.2. Map of the three plots sampled.

Three study sites were chosen in the area surrounding the Kwano Research Centre (see Figure 2.2 above): Two sites close to forest edge (to the southwest of the research centre) which interfaces with the savannah grassland and an internal control site (to the east of the research centre) where all selected trees were over 100 m from the edge of the forest. Although burning is officially discouraged within the National Park it is routinely conducted by local inhabitants, therefore a controlled savannah burn was conducted at the forest edge site closest to an ancient pathway, as it would likely have been burnt by local inhabitants anyway. Fire was set at the edge of the savannah next to the pathway in mid February, and as the forest was still relatively

damp there was no danger of the fire spreading into the forest edge. The fire was left to burn itself out and an inspection was made of the forest edge once the site was safe to do so. It took approximately 2 hours to burn an area of 2.9 ha and a strip of approximately 1 m of vegetation was left unburnt directly adjacent to the forest boundary therefore the trees on the boundary remained unharmed by the burn. This vegetative strip was made up of a greater number of woody plant species and was much denser than the savannah grassland itself, which was the probable cause of its failure to ignite. The second savannah/forest edge site (two areas of savannah 1.1 and 0.6 ha with forest adjacent to and dividing the savannahs) was left un-burnt, and as it was situated ~1 km from the ancient pathway the risk of it being burnt by local inhabitants was low. Eight trees were selected at the burnt savannah/forest edge, nine at the non burnt savannah/forest edge and ten from the internal control plots, chosen using the Visual Tree Assessment (VTA) (Mattheck and Breloer, (1994) – cited in Aldred and Pike (2008)).

VTA was first suggested by Mettheck & Breloer (1994) and uses physical aspects of the tree and immediately surrounding area to assess its fitness for tree climbing. The indicators used in this assessment are listed below (taken from Aldred and Pike (2008));

- Damaged exposed roots leading to instability of the tree
- Basal cavities undermining the trunk foundations
- Soil cracks indicating the heaving of ground that occurs when a tree with an unstable root system moves in the wind
- Loose, flaky branch forks are structurally weak and often associated with internal decay

- Deep V-shaped branch forks are structurally weak and often associated with internal decay
- Break out cavity indicating decay developing in the tissue exposed by branch fall
- Crown die back indicating weakened branches and often symptomatic of high stress in other parts of the tree, ie it may be dying
- Cankers resulting in localised weakening
- Abrupt unnatural looking bends in branch weakened re-growth on previously damaged limb. A re-growth limb never has the structural integrity of the original
- Insect nests are potentially dangerous to the climber, but also may indicate further internal cavities and structural weakening
- Fungal fruit bodies such as bracket fungi on stem are positive indicators of internal decay.

In order to minimise the amount of variation in arthropod community due to tree species only two species of tree were selected these were an unidentified mahogany species and a species of the family Ulmaceae, *Celtis zenkeri*, although no independent verification of this identification was available (see appendix 1 for an index of which species of tree each sample was taken from). As only a single qualified climber would be present during the study great care was taken in tree selection so as to minimise potential risk. The distances of trees from the forest/savannah interface were measured manually with a tape measure and locations of all trees and forest edges were marked with a GPS (Garmin GPSmap 60CSx). The distances of the internal control trees were estimated from GPS measurements using MapSource software.

This methodology does have its limitations, as only one replicate of each habitat site is being used. However with the limitations of tme, equipment and man power that this study has, there is only time enough for a single habitat replicate.

2.3.2 Climbing Equipment and Tree Rigging

As physical access to the canopy was required for sampling the researcher was trained prior to field work in Basic Canopy Access Proficiency (BCAP) by Canopy Access Ltd during October 2008. This allowed the researcher to safely and efficiently climb trees with minimal risk to him or to the trees. The BCAP method utilises a combination of tree climbing techniques taken from the world of arboriculture and "Working at Height" protocols which enlist all aspects of UK health and safety law.

Once a VTA has been conducted on the chosen tree the next priority is to find a suitable ground anchor. As the sites are within forest areas, smaller trees are used as anchors. To select a suitable anchor tree a VTA was conducted on smaller trees with a Diameter at Breast Height (DBH) of roughly 20 cm within the vicinity of the climbing tree. The anchor system consists of four tree straps (120 cm in length), four steel karabiners and two Petzl GRI GRI pulleys (see Fig 2.3 below). Two of the tree straps are connected via the karabiners to the GRE GRE's and each of the climbing ropes connected to one of them. Each of the climbing ropes is then attached to one of the other two tree straps via the karabiners using an alpine butterfly knot. The main weight of the climber is held on the pulleys with the second two straps acting as a back up in case of equipment failure.

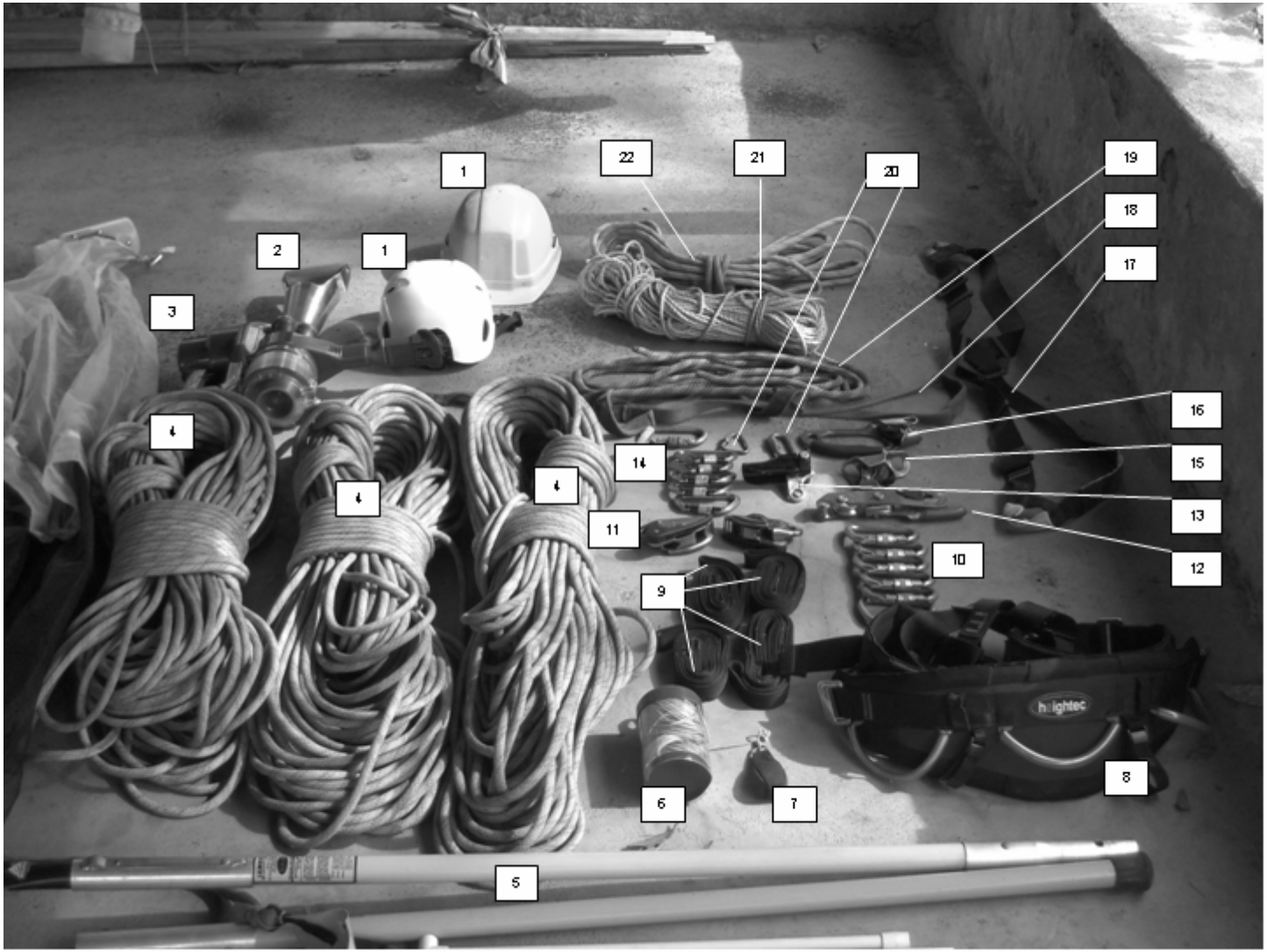
Fig 2.3. Ground anchor set up

In order to place the climbing ropes into the tree a smaller high strength throw line (Samson® Zingit Throwline) is placed over the selected branch. The throw line has a small 250 g throw bag (Weaver® Throwbag 250 g) attached at one end which is then propelled into the canopy using a large sling shot (Jameson® Big Shot). Once the throw line and bag are in the correct position they are lowered down over the selected branch, the throw bag removed and two 100 m semi static climbing ropes (Heightec® low stretch static rope 10.5 mm) are attached using a series of clove hitches. Then using the other end of the throw line the two climbing ropes are pulled into the canopy and back down to the forest floor.

At the ground anchor there is another 100 m climbing rope flaked into two 50 m piles. Each end of this rope was fed through a separate pulley and then attached to one of the climbing ropes using a double fisherman's knot (see above for correct ground anchor selection protocol). This third rope forms the bases of a ground rescue system should the researcher get into difficulties whilst climbing the tree. The system works by providing an additional 50 m of rope that will lower the climber safely out of the tree. A field assistant is constantly present on the ground and fully trained in the use of the rescue system and the immediate medical treatment that is

required after such an event. Possible medical problems include allergic reaction to insect stings and bites, heat related illnesses and suspension trauma.

Ascent and desent of the climbing ropes was achieved through the use of a SHUNT (Petzl fall arrest device), chest ascender, hand ascender and a STOP or I'D (Petzl descent devices) all attached to a sit and chest harness combination, combined using a series of karabiners and personal cows tails (8 mm rope lanyards). For both ascent and descent the SHUNT is placed on the second rope and is used as a fall arrest system, should there be equipment, rope or human error while climbing the main rope. The device locks under applied pressure/friction so if there is a sudden drop the SHUNT will stop fast descent within 1 m of original incident. Ascent of the rope is achieved using a combination of chest and hand ascenders and descent is achieved through the use of the STOP or I'D. During the 2009 field season a STOP was used as the decent device, however the combination of using a STOP and SHUNT as a fall safe system was questioned therefore in 2010 a I'D decent device was used instead. Fig 2.4 (below) shows a full list and illustration of the equipment mentioned in this section.



1. Safety Helmet
2. Soil Extractor
3. Handheld Vacuum
4. 100 m Semi Static Rope
5. Large Sling Shot
6. Throw Line
7. Throw Bag
8. Sit Harness
9. Tree Slings
10. Steel Karabiners x6
11. GRE GRE x2
12. STOP
13. SHUNT
14. Aluminium Karabiners x5
15. Chest Ascender
16. Hand Ascender
17. Chest Harness
18. Foot Loop
19. Personal Cows Tails x3
20. Melange karabiner
21. 50 m Nylon Rope
22. 10 m personal lanyard

Fig 2.4. Climbing and survey equipment

2.3.3 Composite intercept traps

Composite intercept traps (CIT) are a combination of a malaise trap and a flight intercept trap (see section 2.2). Their use in this project was primarily to capture flying Diptera from varying heights within the canopy (see Fig 2.5 below).

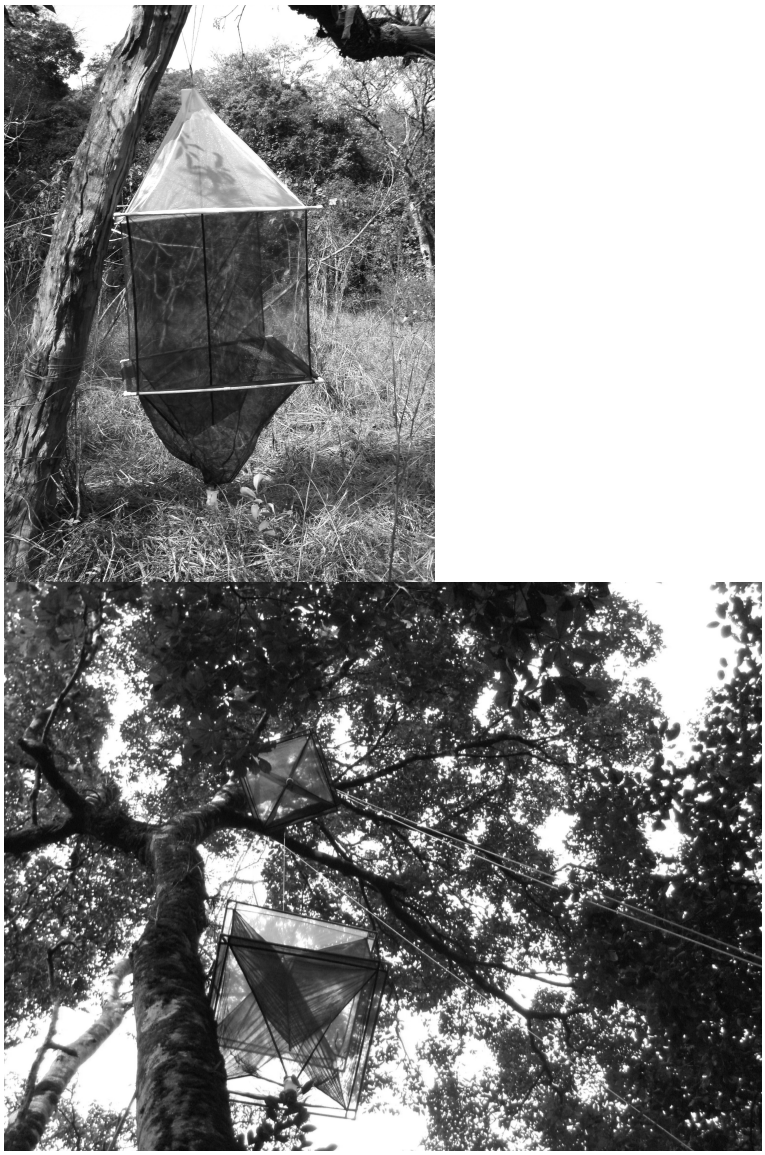


Fig 2.5. Composite Intercept Trap. *Top*: suspended at ground level, *Bottom*: suspended at mid and high canopy levels

In total three CIT's were hung in each of the survey trees for a period of 22 – 23 hrs, therefore potentially capturing all day, night and tourist species of Diptera. The three heights were; ground (with the bottom collector touching or near touching the forest floor), mid canopy (between 10 and 15 m above the forest floor) and high canopy (between 20 and 30 m above the forest floor) (see figure 2.7 below for study design). The height of the high canopy CIT sample was limited by the height that the researcher could safely ascend into the canopy. High canopy CIT's were attached to a suitable branch by use of a 10 m personal lanyard using a combination of knots and karabiners, the mid canopy CIT was hoisted into the canopy using a 50 m nylon rope that the researcher placed over the top branch during the survey. Traps were then removed from the canopy at roughly 22 – 23 hrs later. The collecting jars were half filled (~0.5 lt) with a 50:50 mixture of 100% methylated spirit and water, with a small amount of washing up liquid to reduce the surface tension of the fluid. Once the CIT's were carefully lowered to the ground the contents of the sample collectors was transferred into plastic containers, labelled and carefully packed for transportation back to the research centre. Once at the research centre the samples were removed from the bottles and placed in plastic, labelled sample tubes containing a 70 % methylated spirit solution for long term storage. On returning to the UK the CIT samples were first sorted to order level, then Diptera and Collembola were removed for further analysis. Diptera were identified to family level using McAlpine (1983) and identification of the Calyptrates to genus and species was done by N. Wyatt of the Natural History Museum, London, UK. No other groups were identified further than family level.

2.3.4 Vacuum Samples

As shown in section 1.2.2 Collembola live in a great number of habitats, soil, leaves caves, fresh water and bark. This last habitat is one that might prove to be an interesting habitat to investigate during this study. Rodgers and Kitching (1998) and Shaw et al. (2007)

found that there are a number of arboreal Collembola species associated with bark and leaves. Therefore in order for this thesis to represent a substantial area of Collembolan habitat it was necessary to survey the bark of trees.

Using a vacuum to sample arthropods is a technique that has been used extensively. The equipment used ranges from a modified leaf blower to a purpose built D-VAC sampler (see Sanders and Entling (2011) for a recent review of this methodology). However these forms of equipment are heavy and cumbersome to use in the field, especially when climbing trees. Therefore this study is using a small handheld high powered vacuum cleaner (Dyson DC30, see figure 2.6 below) to sample for non flying arthropods present on the bark of trees.

Fig. 2.6, High powered handheld vacuum.

Due to the relatively untested nature of this equipment a small pilot project was initiated prior to the start of field work. Six one minute samples were taken from trees situated within the grounds of Whitelands College, Roehampton University, in December 2008. The samples were then sorted to order and abundance of Collembola noted. Considering the time of year, the presence of any Collembola was rare. However Collembola were found within all the samples, including three species of *Entomobrya* (*Entomobrya*

albocincta, *E. nivalis* and *E. multifasciata* according to Hopkin (2007), but the '*nivalis*' was in fact *E. intermedia* (Gisin, 1960) (P. Shaw, pers. Comm). Therefore it was considered that this technique using this small vacuum cleaner was a viable option for sampling the bark of trees in Nigeria.

The sampling protocol in the field was developed during the pilot phase of the field work in early January 2009. A total of three samples were taken from each survey site. One from the base of the tree, ~1.3 m above the forest floor, a second from ~10 m above the forest floor and a third from the high canopy (>20 m from the forest floor), each sample was taken from roughly the same height as the CIT samples (see figure 2.7 below for study design). Height and survey site were recorded for each sample, each sample was preserved in 70% methylated spirit and carefully stored for transport. During the sampling process the handheld vacuum was moved over an area of roughly 50 x 50 cm, using the 'brush' adapter and gently moved in an upward direction over the sample area for a period of 1 minute. The sample was then immediately transferred into a clear plastic bag, labelled and taken back to the research camp for final storage preparation.

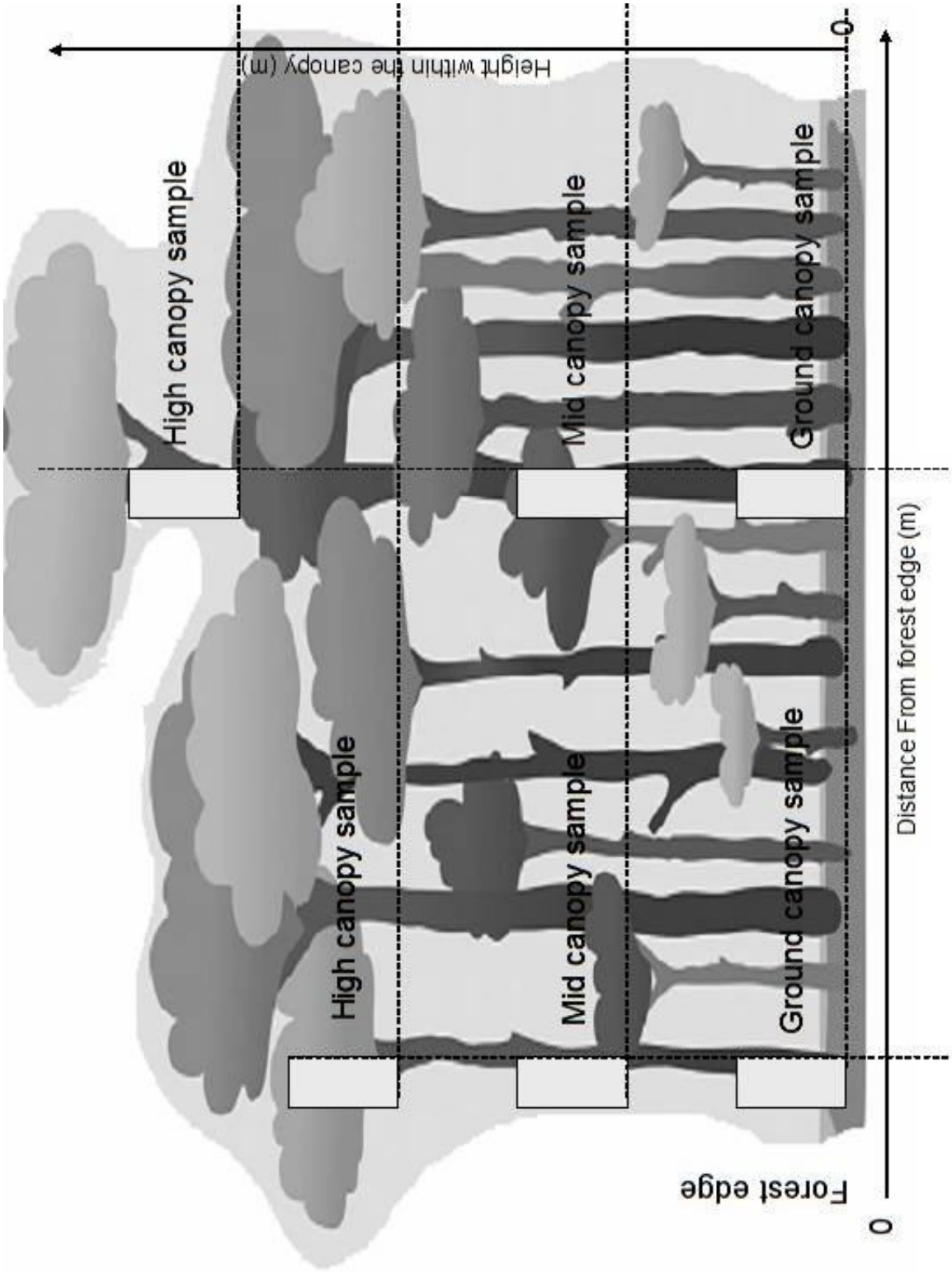


Figure 2.7. Study design; three CIT/vacuum samples taken at each tree, at three different heights, ground soil samples taken from the base of each tree and suspended soil samples taken as encountered in the vertical column.

2.3.5 Soil Samples

Another important habitat for Collembola is soil. Therefore in order to sample a diverse range of Collembolan habitats soil must be accounted for. As this study is researching vertical stratification soil samples must be taken from as many areas of the vertical gradient as possible. Winchester (2002) proposes a quantitative method for surveying arboreal soil arthropods, where samples are taken from not only the forest floor but at numerous positions throughout the canopy, both at the main trunk and into the wider canopy. However this technique requires climbing equipment and techniques that were not available for this thesis, thus a modified sampling protocol will be used.

Soil is to be collected at the forest floor and from suspended soil/leaf litter encountered in the canopy. A small 5 x 7 cm bulb planter was used to remove soil from the forest floor (2 pseudo samples) and placed in a clear plastic bag. Suspended soil was removed by hand in an inverted clear plastic bag. Samples were labelled by site, height and distance from the edge (where applicable) and taken back to the research camp. Once at the research camp arthropods were extracted using Winkler Bags (see section 2.2 for details of this methodology). Samples were left for a period of seven days in a covered airy position to dry and arthropods extracted. The arthropods are then removed to plastic samples tubes, labelled and stored for transportation. The remaining soil is weighed and left to dry for a further seven days when it is weighed again so that a measurement of arthropods per dry mass can be calculated.

Fig 2.8. Winkler Bags suspended under cover at Kwano Research Centre.

Winkler bags (see Figure 2.8 above) were used in preference to Tulgren funnels as the required power supply for the Tulgren funnels could not be met at the research camp. Other methods such as floatation extraction were considered but the required chemicals were not available in country and could not be easily imported from the UK.

2.3.6 Habitat surveys

Throughout the previous chapter biotic and abiotic habitat parameters have been shown to play and important role in determining arthropod abundance and density, and these parameters will change along both horizontal and vertical gradients. Therefore a quantitative and repeatable habitat survey had to be undertaken to understand the underlying factors that are driving any possible changes in arthropod abundance, density and diversity along both these gradients.

To survey the whole array of habitat parameters of a tropical forest would be a long and time consuming task, therefore this project only studied a select few factors that this literature suggests to be important. Heterogeneous habits have been shown to provide a resources and habitat niches for arthropods often resulting in increased diversity and

abundance. Therefore to survey for heterogeneous qualities of the forest this project followed a modified methodology from Fayle et al. (2009) and Dial et al. (2006), where the distance from a single point within the forest to the nearest vegetation is measured over a 360º arc, taking measurements every 30º. Each of those measurements are categorised under one of five habitat descriptions (tree foliage, liana foliage, woody, edge/open and dead). These habitat descriptions take into account many of the resources that the arthropods will need in order to survive within the habitat. Therefore rather than simply relying on height or distance from the edge as the only determinants of possible change in arthropod assemblage, habitat structure and heterogeneity were also taken into account.

The procedure followed closely that of Fayle et al. (2009) and Dial et al. (2006) and will measure habitat heterogeneity at both forest floor and throughout the vertical gradient surveyed. The methodology differ from that of Fayle et al. in that rather than using a transect, survey points were based around a single tree survey site so that direct comparisons between arthropod assemblages and habitat parameters can be drawn. At each tree four points will be surveyed at ground level 10 m from the base of the tree on north, south, east and west coordinates. Measurements of the same nature will also be taken in the vertical column at each survey height (including an additional ground canopy sample from the base of the tree).

2.3.7 Environmental Data

As shown in Chapter 1 environmental considerations must be made when investigating both edge effect and vertical stratification. To that end it is necessary to measure these parameters in order to get a clear picture of the microclimatic changes that occur in the forest, and draw conclusions on their effect on the abundance and richness of the taxa that are being studied in this thesis.

In Chapter 1 ambient temperature and rain fall/humidity were shown to be particularly important to collembolan distribution and abundance. Therefore these three parameters were measured during sample collection. The Kwano field station has had a permanent weather station recording data for the past decade, although the humidity and temperature will vary within the forest, the rainfall measured at this site will be an adequate approximation, as all sites are within 2 km of the recording station. The rain is recorded by a rain gauge situated in open ground at the research centre. Rain fall was recorded prior to trap removal each morning, so that a measure of the previous 24 hr period can be determined.

As the survey sites were situated under forest canopy the relative temperature and humidity differed from the ambient measurements recorded at the weather station; therefore data loggers (Tinytag Plus2) were installed at the same points as the CIT's. The data loggers recorded relative temperature and humidity every eight minutes over the 24hr period that the CIT's were set, therefore direct conclusions can be drawn for the effects of these environmental factors on Dipteran and Collembolan communities.

2.4 Methodology Conclusion

From the information discussed in the literature review it has been shown that there are many potential factors that may impact the abundance and richness of the study species. Therefore this methodology has been designed to incorporate as many of these factors that can practically be measured given the time and resources of this study (limited possible field seasons and a single researcher). The data gained will give a clear picture of the environment and habitat that the focal taxa inhabit, and should help identify spatial and

environmental parameters that are important in determining the abundance and richness of these arthropods within this West African forest.

This chapter has not discussed statistical methodology in any great detail; however certain methodologies have been mentioned. There is a detailed statistical methodology in Chapter 3 (sections 3.2 and 3.3.3.2), which shows, among other methodologies, how the linear and non linear regression models proposed by Ewers and Didham (2006) will be used in this thesis.

Chapter 3: Analyses of ordinal abundance and changes in scope of project

3.1 Introduction

To understand the complexities of the data that were collected during the field campaign, and how they relate to the questions asked in this thesis, it is first necessary to investigate the trends that are present within the data. Therefore in this chapter the organisation of the dataset will be discussed. The chapter will then concentrate on how the vertical stratification, burning treatment, edges effects and the changing of seasons from dry to wet affect the total abundances of Diptera and Collembola.

Chapter 1 reviewed information and analysis of previous studies in these taxa; however, possible statistical analysis for the dataset was not discussed in any great depth. Due to the discrete nature of the data categories it should be possible to analysis these data with a combination of parametric comparison statistics such as ANOVA and t-tests or their non parametric counterparts. However, there is also the opportunity to use correlation and regression analysis to discover the properties of any edge effects present, as distance from the edge of the forest forms a gradient that invertebrate abundance and environmental factors can be fitted to. To this end this chapter will introduce the main statistical methodologies that will be used in this thesis.

The data collection methodologies outlined in Chapter 2 concerning the collection of dipteran samples was successful in producing sufficient samples for analysis; however, Collembola collection methodologies were not so successful. The use of a handheld

vacuum to collect samples from the bark of the trees resulted in no Collembola being sampled, even though pilot tests in the UK did produce results. Collemboa from soil samples also proved to be unsuccessfully extracted in the field, but whether this was due to there being no Collembola present in the soil or that the Winkler bags used to extract them were unable to do so is not clear. No individuals were collected in the dry season of 2009, and fewer than 10 individuals were collected in the 2009 wet season. Thus the use of these methods was discontinued for the final wet and dry season campaign in 2010.

As there is no baseline knowledge of the Collembola population within this region of West Africa, there are no other studies to compare these results with. However, there were Collembola within the habitat as the Composite Intercept Traps (CIT) did yield individuals. A total of 582 individuals were collected from the CIT's over all sites and all seasons, with a majority sampled in the wet season. This constitutes a dataset that can be analysed using discrete categories of height, distance from the edge, treatment and season. Therefore it is these results that will be analysed in this chapter. However due to the small nature of the dataset no further analysis of the Collembola will be conducted in the rest of this thesis.

3.2 Methodology

The aim of the initial phase of data collection was to establish a working methodology that would result in the collection of a robust dataset. In Chapter 2 several methods were outlined, and the previous section discussed the success or failure of those methodologies at the study site. Therefore the samples successfully collected will now be analysed. Field collection started in January 2009, with the initial dry season phase completed in March 2009. The first wet season campaign ran from the beginning of June 2009 until the end of

July of the same year. In order to achieve sufficient replication a third sampling campaign ran from March until July 2010, which incorporated both wet and dry seasons. Therefore a total of 36 weeks of field collection was completed for this project. 253 CIT samples were collected from 36 individual trees across three sample areas (burnt, non burnt and internal control). Each tree consisted of a ground, mid and high canopy sample, and each tree was sampled between 2 and 4 times between January 2009 and July 2010. In the 2009 sampling season 38 additional CIT samples were taken from the adjacent savannah. In the dry season, samples were taken from the non burnt savannah and then two sets of samples from the burnt savannah pre and post burn, therefore a total of three habitats were sampled. In the wet season samples were again taken from the non burnt savannah, but as the burning treatment had already occurred, post burn samples could only be taken therefore only two habitats were sampled (see appendix for full list of sites and co-ordinates)

All statistical analysis was conducted in SPSS 17 unless otherwise stated. Initially total Diptera abundance and total Collembola abundance (2009 and 2010 data combined) were analysed for normality using a one sample Kolmogorov-Smirnov test. Where datasets showed a non normal distribution the data were transformed using a $\log_{10}(x + 1)$ transformation. If data were still non normal, non parametric tests were used on the untransformed data.

The dataset was initially coded according to canopy strata, treatment condition and season (wet and dry). Then other parameters were introduced such as maximum and minimum temperature and humidity, rain (in mm and presences or absence) and also discrete distance from the forest boundary. Table 3.1, below, lists all these categories. Environmental parameters (humidity and temperature) were only recorded in the 2010 dataset however rainfall was recorded in all years.

Table 3.1. Categorical, temporal and environmental variables.

Season	Canopy Height	Treatment	Distance from the edge (m)	Rain (mm)	Temperature (°C)	Humidity (RH%)
Wet	Ground	Burnt	5-10	0 (no rain/dry season)	16-19	0-10
Dry	Mid	Non Burnt	11-15	1-10 (light/short showers)	20-23	11-20
	High	Internal Control	16-25	11-30 (heavy showers)	24-27	21-30
			26-40	31-40 (prolonged heavy rain)	28-31	31-40
			41-60		32-35	41-50
			61-80		36-39	51-60
			Internal Plots		40-44	61-70
						71-80
						81-90
						91-100

Datasets were split between categories in order to achieve a finer scale of results and in some cases these data sets did not prove to have a normal distribution (tested with a Kolmogorov-Smirnov test). In these cases non parametric tests were used. For paired comparisons a Mann-Whitney U (MW) test was used and for multifactor analysis a Kruskal-Wallis (KW) test was used. Where the KW test showed significance within the dataset a post hoc MW test was employed with all combinations of factors compared. In cases where type two errors were likely to occur (multiple MW post hoc tests) a Bonferroni correction was applied. The equation used for Bonferroni correction was;

$$\alpha_{new} = \frac{\alpha_{old}}{C}$$

Where α_{old} = the original significance level, α_{new} = the corrected significance level and C = the number of comparisons to be made. Where MW tests analysed a sample set of >41

samples the z-approximation score is reported as the test statistic (shown as '*z*'); however, where sample size was <41 the '*U*' statistic is reported (Green and Salkind, 2008).

Initially correlation analysis of the edge effects takes the form of a Spearman's Rank correlation. A Spearman's correlation was chosen not as a non parametric alternative for non normal distribution, but because the relationships that are to be detected maybe monotonic but not linear and therefore a Spearman's rank correlation is a safer test. Detailed methodology regarding the linear and non linear regression analysis can be found in section 3.3.3.2.

3.3 Results

3.3.1 Collembola preliminary analysis

3.3.1.1 Collembola spatial analysis

Total Collembola abundance data were not normally distributed, and a $\log_{10}(x+1)$ transformation did not correct this. Therefore data were analysed using non parametric tests. Between season variance was analysed with a MW test. The results showed that the wet season had a significantly higher abundance than the dry season, $z = -8.203$, $p < 0.001$. Figure 3.1, below showed the magnitude of this difference.

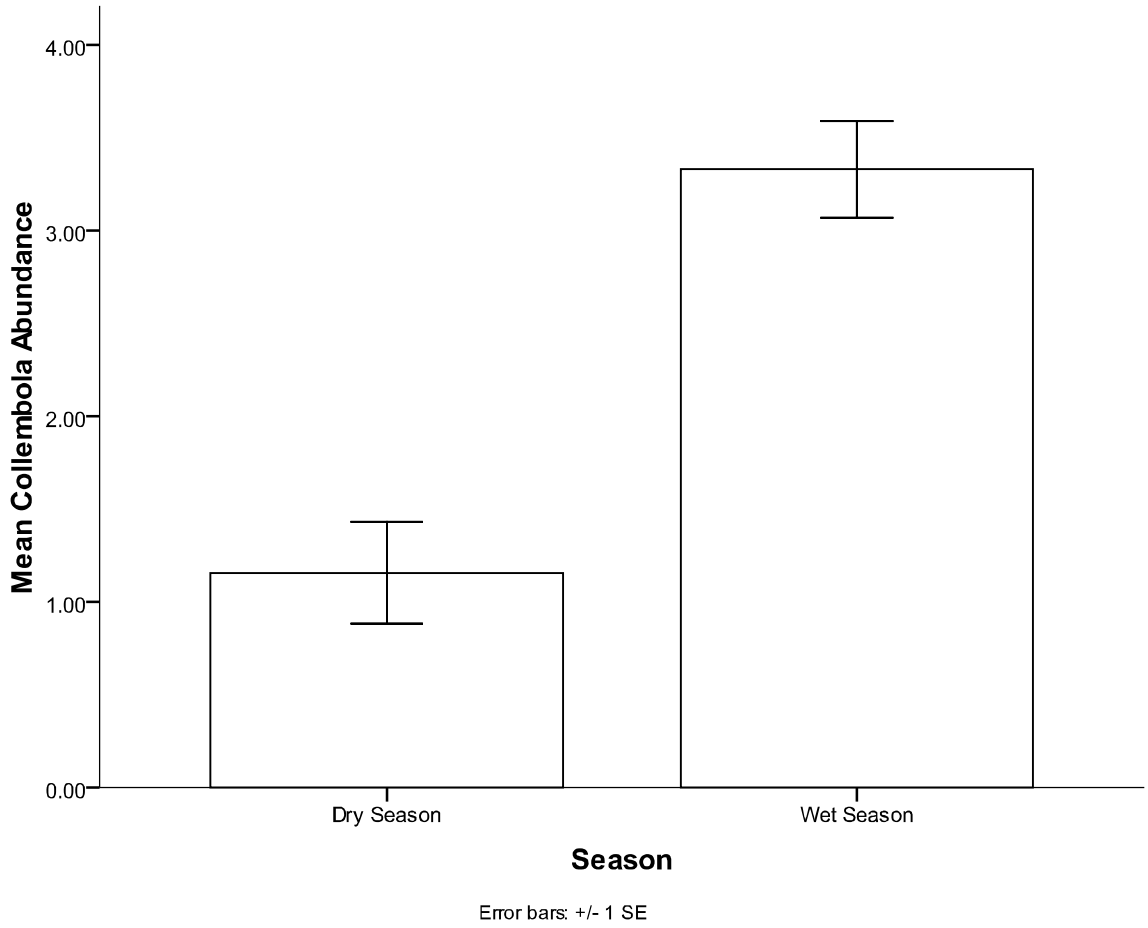


Fig 3.1. Seasonal difference in Collembola abundance (per trap day), in the Kwano forest

The data were split by season to analyse possible differences in treatment sites (burnt, non burnt and internal control). In both the dry and wet season the KW test showed there to be a significant difference between treatment sites ($H = 19.11$, $df = 2$, $p < 0.05$, and $H = 11.52$, $df = 2$, $p < 0.05$, respectively). Therefore both wet and dry seasons collembolan abundance were tested post hoc with Mann-Whitney tests.

As multiple comparisons were to be made a corrected p value of 0.016 was used to detect significance. In the dry season the burnt edge had significantly lower abundance than both the non burnt edge, $z = -3.43$, $p < 0.016$, and the internal control plots, $z = -4.30$, $P < 0.016$, but there was no significant difference between the non burnt edge and the internal control plots, $z = -1.26$, *ns*. In the wet season there was no significant difference between the burnt and non burnt edge, $z = -0.64$, *ns*. However the Collembola abundance was significantly

lower in the internal control plots than both the burnt edge, $z = -4.30$, $p < 0.016$, and the non burnt plots, $z = -2.78$, $p < 0.016$. Figure 3.2, below shows these differences.

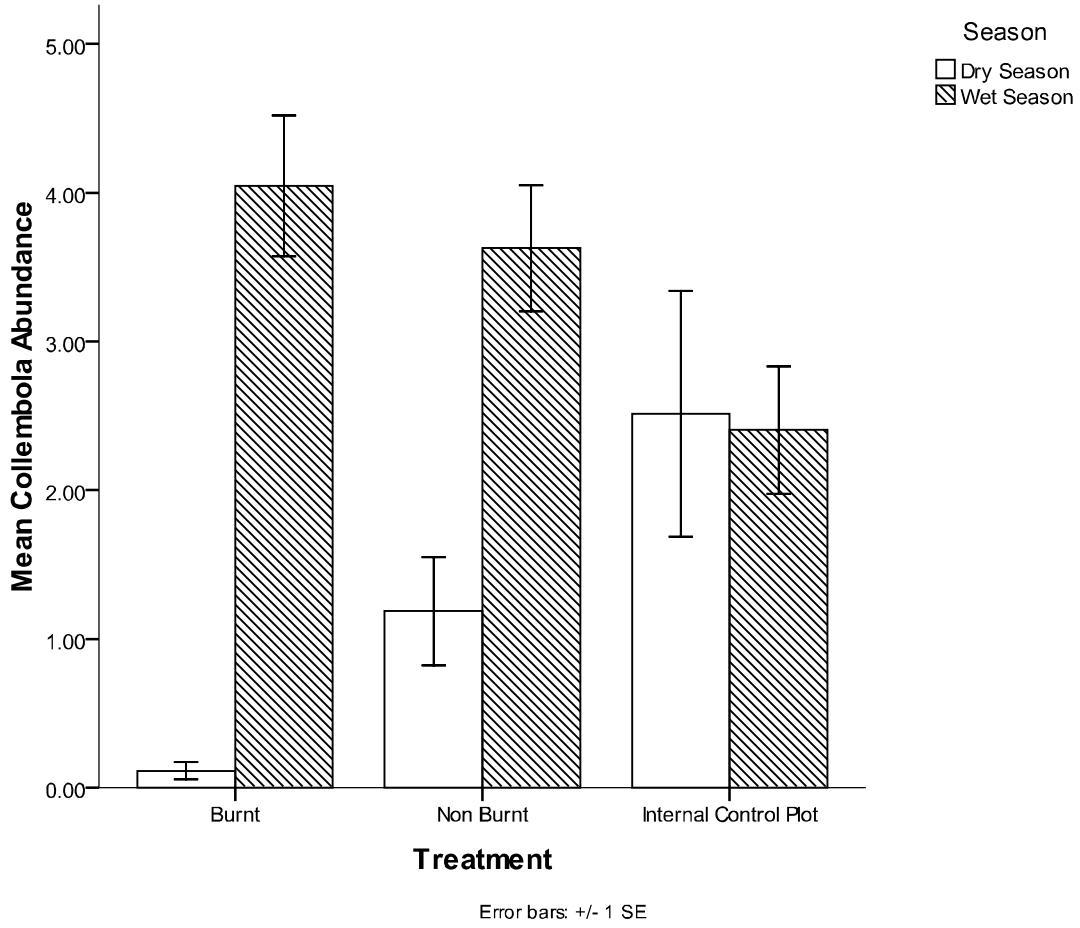


Fig 3.2. Comparison of collembolan abundance (per trap day) under three treatments in the dry and wet season, Kwano forest.

The data were now split between treatments and analysed for seasonal changes with a MW test. As only one comparison was being made no correction was necessary. There was no significant difference between abundance in the internal control plots between wet and dry season, $z = -1.18$. However at both the burnt edge, $z = 7.44$, $p < 0.05$, and the non burnt edge, $z = -5.23$, $p < 0.05$, Collembola abundance was significantly higher in the wet season (see fig 3.2 above).

Differences between height categories were now analysed by the same method. Data were split between seasons and the data analysed with a KW test. Neither the dry season, H = 2.71, df = 2, *ns*, or the wet season, H = 2.55, df = 2, *ns*, showed any significant differences between height categories, therefore no post hoc analysis was conducted for either season. The data were then split by height category and seasonal differences analysed. The ground, z = -4.98, $p < 0.05$, mid, z = -4.10, and high canopy, z = -5.09, $p < 0.05$, all had higher abundances in the wet season (see fig 3.3 below).

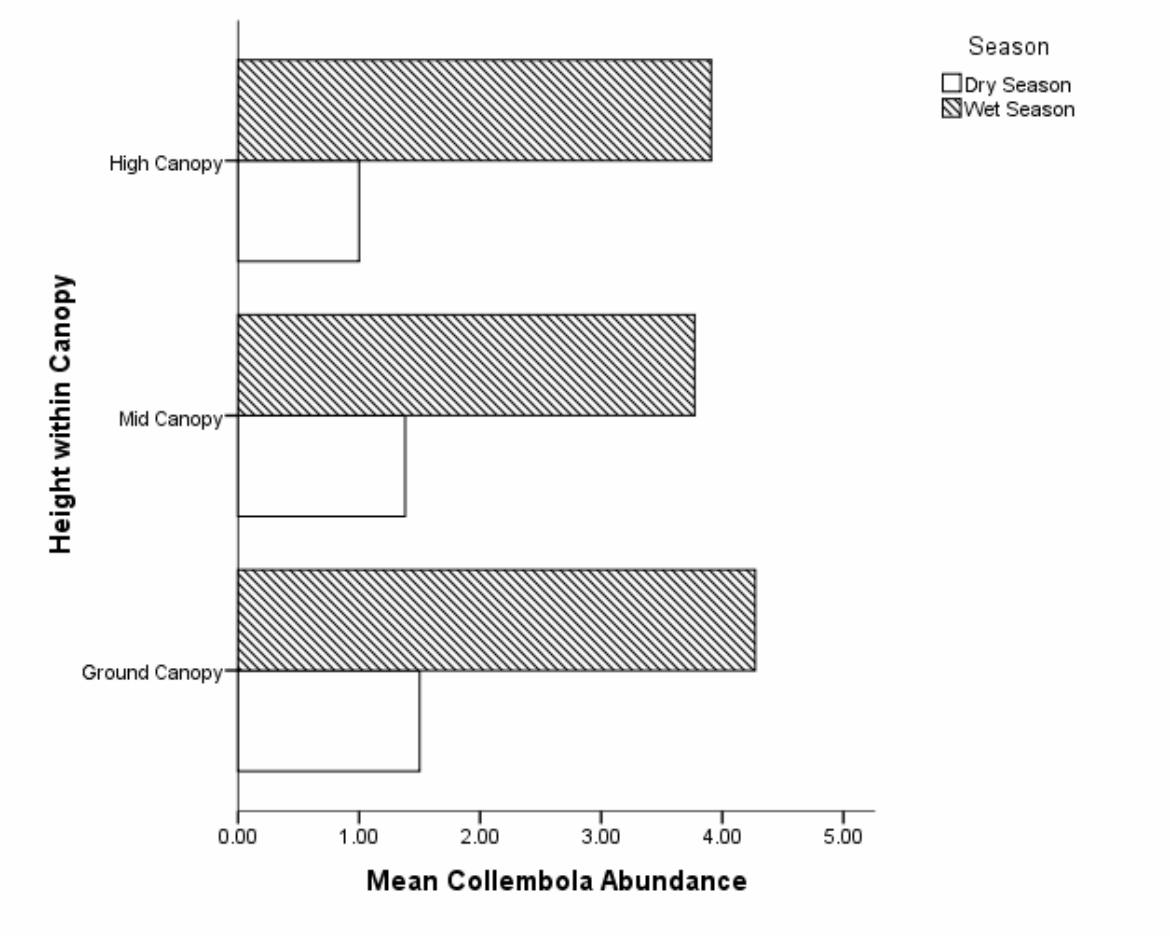


Fig 3.3. Comparisons of collembolan abundance (per trap day) at three height categories in the wet and dry season, Kwano forest.

Due to the fact that there are seven categories of distance from the edge (see table 3.1) using multiple MW post hoc tests to analyse the edge effect would result in a corrected p value too small to be visible in SPSS output. Therefore a Spearman's correlation between

the measured distance from the edge and Collembola abundance was performed with the data split between seasons. Neither the dry season, $r_s = 0.045$, *ns*, or the wet season, $r_s = -0.014$, *ns*, showed any significant correlation between distance from the edge and Collembola abundance.

3.3.1.2 Environmental Analysis

A difference ($H = 18.787$, $df = 4$, p=0.001) in Collembola abundances was found between maximum and minimum temperature categories. There were no results for the 16-19 and 20-23 ºC categories so they were therefore removed from the analysis. Fig 3.4, below, shows the box plot of the remaining categories. From it we can see that there is a clear split between samples whose maximum temperature ranged between 32-44 ºC and those that ranged between 24-31 ºC. These two ranges denote wet (24-31 ºC) and dry (32-44 ºC) season maximum temperatures. So as not to increase the probability of type 1 errors for post hoc analysis three comparisons were selected to detect significant differences between groups, thus our corrected p value was 0.0167. As the medians of the 24-27 and 28-31 ºC were very similar, only 24-27 ºC was used to compare to all three dry season groups (32-35, 36-39 and 40-44 ºC).

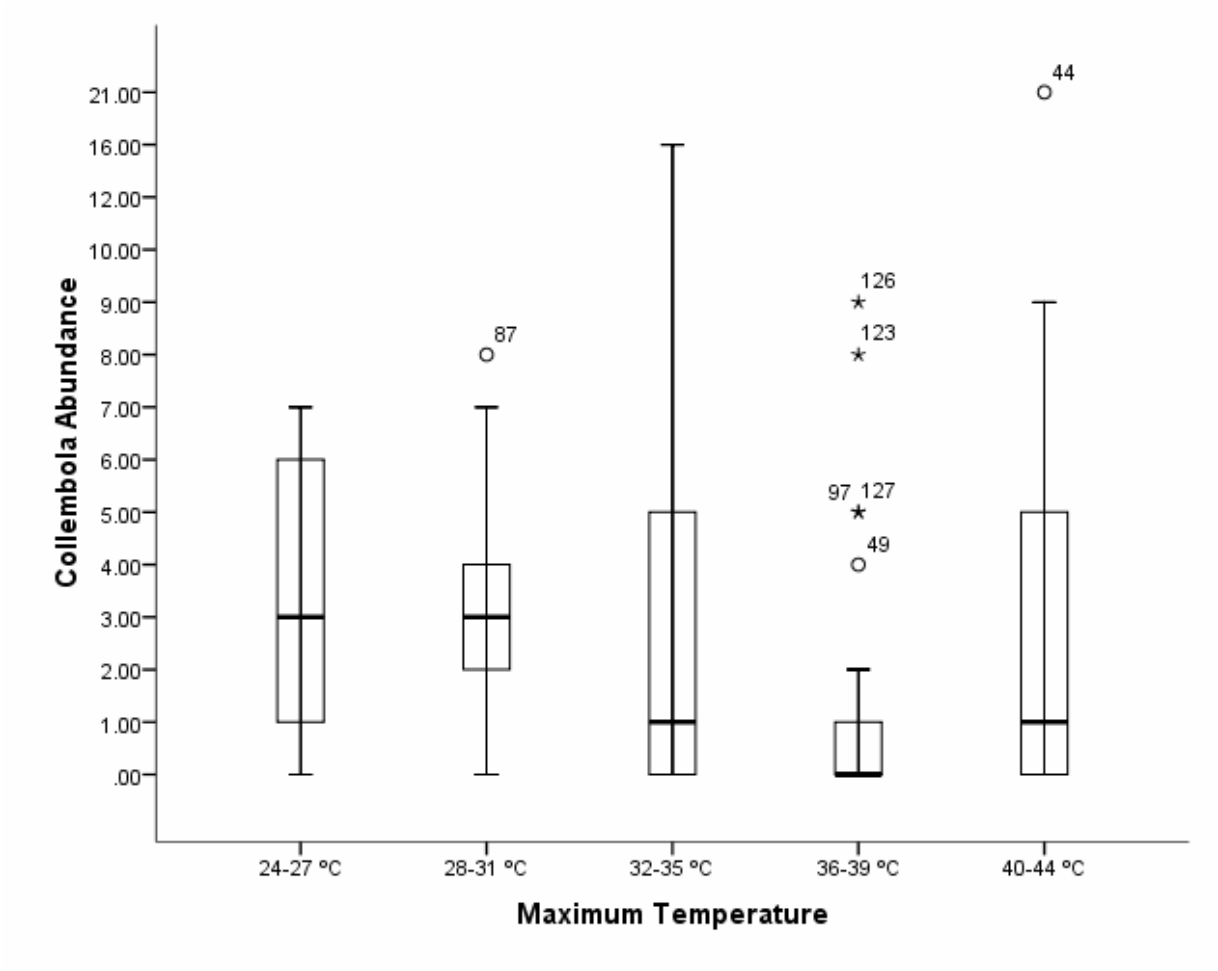


Fig. 3.4. Boxplot of collembolan abundance (per trap day) against maximum temperatures, in the Kwano foorest.

Collembolan abundance did not differ significantly between wet season (24 -27 ºC) samples and samples with maximum temperatures of 32-35 ºC, $U = 220$, ns, or with maximum temperatures of 40-44 ºC, $U = 37$, *ns*. However the Collembola abundance at 24 - 27 ºC was significantly higher than samples with a maximum temperature of 36-39 ºC, $U = 79.5$, $p = 0.001$.

The same analysis was conducted on minimum temperature. Out of the 7 temperature categories only two contained data, namely; 16-19 and 20-23 ºC. The Kruskal-Wallis test showed there to be a significant higher collembolan abundance in the 20-23 ºC category, $H = 11.891$, $df = 2$, $p=0.003$ (see fig 3.5 below).

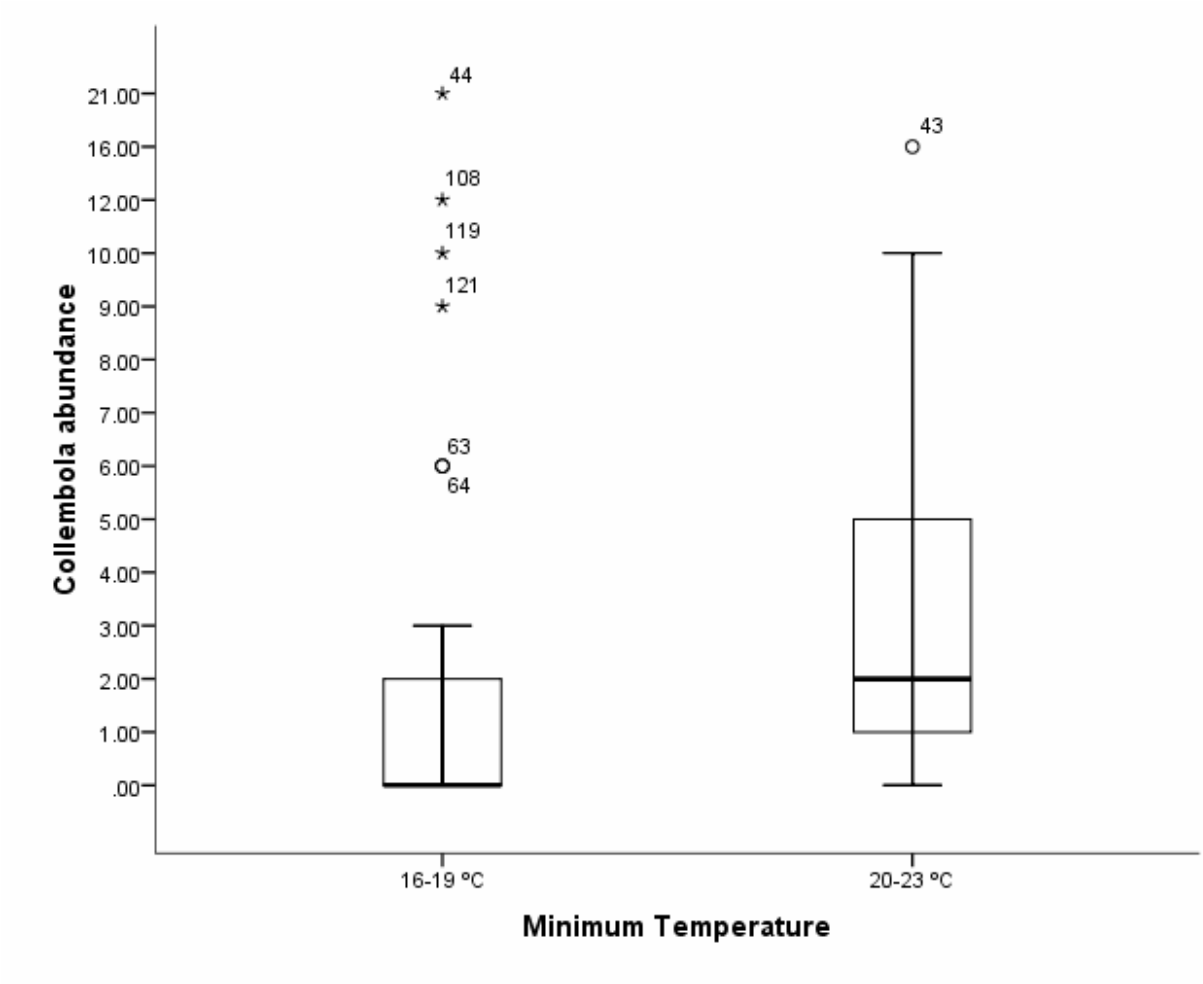


Fig 3.5. Boxplot of collembolan abundance (per trap day) against minimum temperature, Kwano forest.

Only one Mann-Whitney host hoc test was conducted therefore no Bonferroni correction was necessary. There was a significant difference between these two categories, U = 1033.5, z = -3.241, p = 0.001, r = -0.289. As with the maximum temperature data these two groups represent wet season (20-23 ºC) and dry season (16-19 ºC), therefore showing a significant difference in seasonal abundance.

Humidity data were also recorded as maximum and minimum during the time period of the trap, and were split into discrete categories (see table 3.1 for category list). The Kruskal-Wallis test showed that there were significant differences within the minimum humidity data set, H = 36.143, df = 9, p<0.001 (see fig 2.5 for boxplot). For post hoc analysis the categories were split into three distinct groups for comparison, low humidity (0-30 RH%),

medium humidity (31-60 RH%) and high humidity (61-100 RH%). From each of these three groups one category was chosen for post hoc comparison, therefore the corrected p value was 0.016. The categories chosen were 21-30 RH% (low humidity), 51-60 RH% (medium humidity) and 81-90 RH% (high humidity).

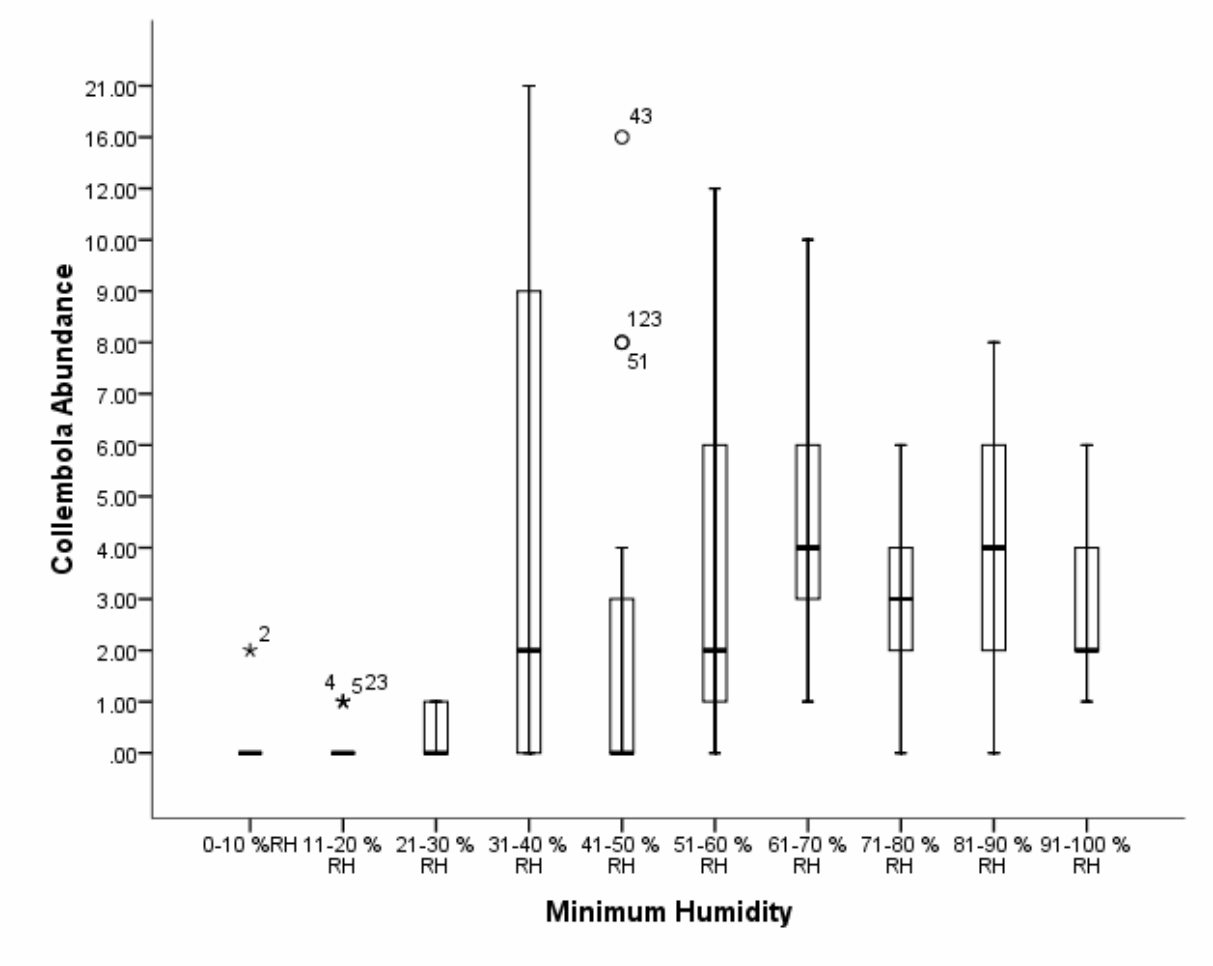


Fig. 3.6, Boxplot of collembolan abundance (per trap day) against minimum humidity, Kwano forest.

The post hoc Mann-Whitney Tests showed that there was a significant difference in collembolan abundance between the low humidity categories and medium humidity categories, $U = 12.0$, $p < 0.016$, and between the low and high humidity categories, $U = 4.0$, $p < 0.016$, $r = -0.715$. However there was no significant difference between medium and high humidity categories, $U = 89.5$, *ns*.

There were no recordings of maximum humidity under 50 RH% therefore only categories within the 51-100 RH% range were analysed. The analysis showed that there were significant differences within the model, $H = 43.047$, $df = 4$, $p < 0.05$. The category 91-100 RH% represents the majority of wet season samples, therefore this was used to compare to dry season (51-70 RH%) and semi-wet season (71-90 RH%) samples (see fig 3.7 below)

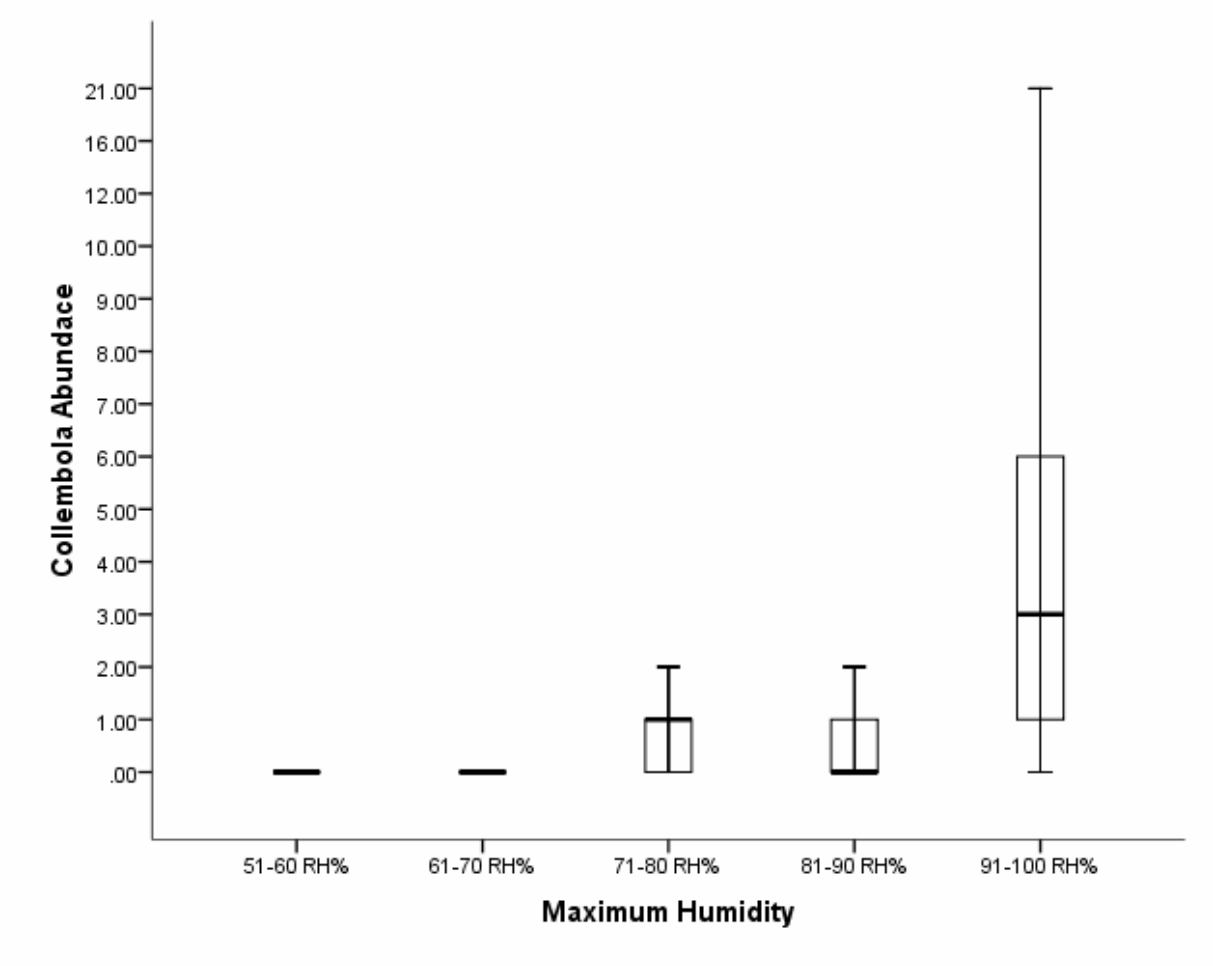


Fig 3.7, Boxplot of collembolan abundance (per trap day) against maximum humidity, Kwano forest.

A total of three post hoc Mann-Whitney tests were applied and therefore a Bonferroni corrected p value of 0.016 was used. The comparisons represented the least distance between medians, therefore 91-100 RH%, 71-80 RH% and 61-70 RH% were chosen for comparison. There was a significant difference in collembolan abundance between 91-100

RH% and 71-80 RH%, $U = 139$, $p < 0.016$, and between 91-100 RH% and 61-70 RH%, $U = 102$, $p<0.016$. There was no significant difference between 61-70 and 71-80 RH%, $U = 24$, *ns*.

The last environmental parameter for analysis was rainfall. The Kruskal-Wallis test showed there to be significant differences within the model, $H = 35.746$, $df = 3$, $p < 0.05$ (see fig 3.8 below).

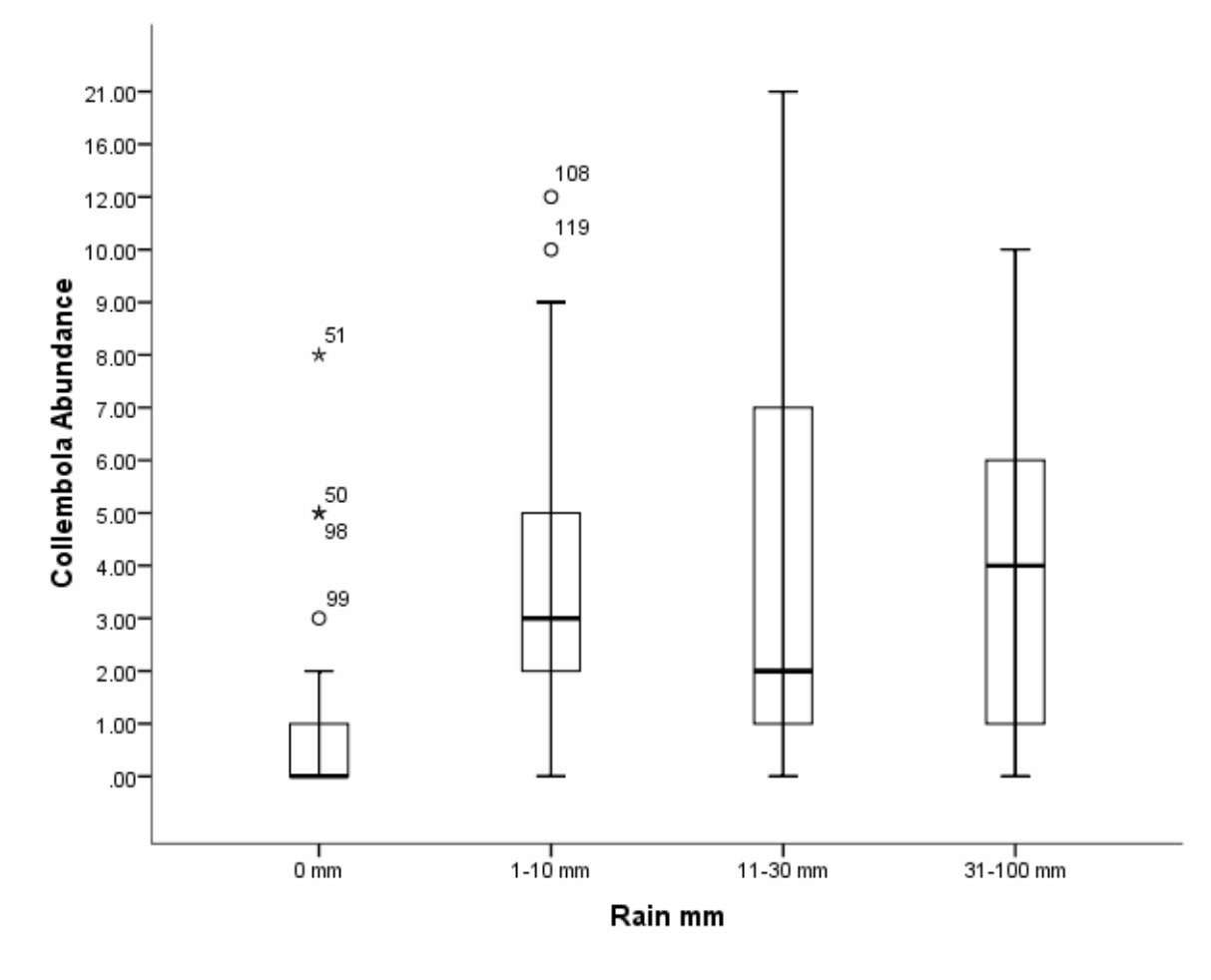


Fig. 3.8.. Boxplot of collembolan abundance (per trap day) against rain (mm), Kwano forest.

A total of 6 Mann-Whitney tests were used as post hoc analysis to test for significance between groups, therefore a corrected p value of 0.008 was used to reduce the risk of type I errors. The post hoc analysis showed that samples representing the dry season (0 mm)

were significantly different from the other three groups; light/short showers ($U = 420$, $p < 0.008$), heavy showers ($U = 134$, $p < 0.008$), and prolonged heavy rain ($U = 120$, $p < 0.008$). There were no significant differences in abundance between periods of light/short showers and heavy showers ($U = 411.5$ *ns*) or light/short showers and prolonged heavy rain ($U = 362$, *ns*), and there was no significant differences in abundance between periods of heavy showers and prolonged heavy rain ($U = 86$, *ns*).

3.3.1.3 Conclusions for Collembola Analyses

It is clear from the data analysed that the Collembola in the canopy at Gashaka are significantly affected by seasonality, with abundances significantly higher during the wet season than during the dry season. Adaptation to short periods of drought by Collembola has been shown in European soil associated species (Kaersgaard et al., 2004), however, adaptation by tropical canopy associated species is not well known. Kærsgaard et al. (2004) tested the roles of cuticle, osmolytes and water reserves in nine species of European Collembola; representing euedaphic, hemiedaphic and epedaphic forms. The authors concluded that forms from each of the soil layers used a combination of these three biological aspects (characteristics) along with behavioural adaptations in epedaphic species in order to survive drought periods. The experiments were designed to investigate a reaction to a short intense period of drought (5 – 7 days), whereas this study deals with a prolonged period of drought lasting three to four months. Therefore it could be assumed that the Collembola present within this Nigerian tropical forest system have evolved both biological and behavioural adaptations to survive the long dry periods.

From the data presented in this section there is a significant positive association between collembolan abundance and wet season environmental conditions (high humidity and high rainfall), with very few records of active Collembola during the dry season. Seasonal

behavioural adaptation in Collembola has been shown in more temperate environmental conditions. For example in Central Japan *Xenylla brevispina* were shown to migrate from the canopy to the soil during the winter months (Yoshida and Hijii, 2006). Although both microhabitats held populations of this species the year round, the annual shift in population density was significant. Prinzing (1997) showed that even on the microhabitat scale, *Entomobrya nivalis* living in Northern Germany maximise their environment and food sources even within the crevasses of bark. Therefore one may suggest that similar coping strategies are being employed in the tropics, although not through cold adaptation but drought adaptation.

The conclusions drawn here merit further and more detailed investigation, as it is apparent from the literature that tropical collembolan adaptations have not been studied thoroughly. The data presented here and in previous studies into temperate and boreal species of Collembola suggest that Collembola can adapt and therefore evolve to cope with extremes in environmental conditions whether it is through biological adaptation as seen in soil associated species or by behavioural adaptation as shown in *X. brevispina* and *E. nivalis*. However due to the extensive amount of work and resources that would require it would be inappropriate for this project to pursue this hypothesis. Therefore this thesis will continue with only Diptera as its focal order.

3.3.2 Diptera Ordinal level Analysis of Spatial Patterns

3.3.2.1Introduction

This section will outline the preliminary results from the dipteran study. Here data will be analysed at a broad scale (ordinal) to investigate underlying patterns in abundance. This initial analysis considers the spatial aspect of the data – environmental factors are taken into account later in the thesis. It can be seen from the introductory chapter, that previous studies have shown the impact of edge, height and anthropogenic effects on invertebrate populations. It is therefore important to start to describe the data collected in these terms.

Initially a pilot study of the surrounding savannah matrix was conducted in order to determine if there were differences in the dipteran abundance between the area to be burnt and the area to be not to be burnt before the treatment experiment began. If a prior difference existed then the results could be confounded by these initial differences and no firm conclusions could be drawn from the data without much more detailed analysis. Following this, an investigation was conducted into spatial patterns in dipteran abundance within the forest.

3.3.2.2 Methodology

In order to ascertain that there were no significant differences in dipteran abundances between the two edges (burnt and non burnt) before the experiment commenced, it was essential to take samples from the savannah matrix beyond the two forest edges. In the dry season three sets of samples were taken; eight from the savannah before it was burnt, eight

from the savannah that was not to be burnt and eight from the savannah three days post burn. In the wet season samples were only taken from the burnt savannah and the non burnt savannah, as the pre burn savannah no longer existed. Each composite intercept trap was hung from available trees at varying distances from the edge of the forest and into the adjacent savannah matrix (0, 10, 20 and 30 m from the edge of the forest). Distances were recorded using a tape measure for further analysis with regression models (later sections); however for this section all samples were pooled. Each trap was left for a period of approximately 24 hours and then samples were removed and stored for further analysis. A total of 24 dry season samples were collected and 16 in the wet season. The collection methods of dipteran samples from the forest follow that set out in the methodology chapter and were the standardised method for all forest sampling for this thesis.

Data were analysed through both parametric and non parametric methods, depending on the normality and the sample size of the collected data. Where the data did not allow for parametric analysis, a Kruskal-Wallis test was used to detect significant differences within the data set. If the data allowed for parametric analysis then a multivariate ANOVA with either Tukey's, Hochbergs GT2 or Gabriel's post hoc tests (dependent on sample size) were used as sample sizes were not equal across all factors. All data were analysed with SPSS V.17.

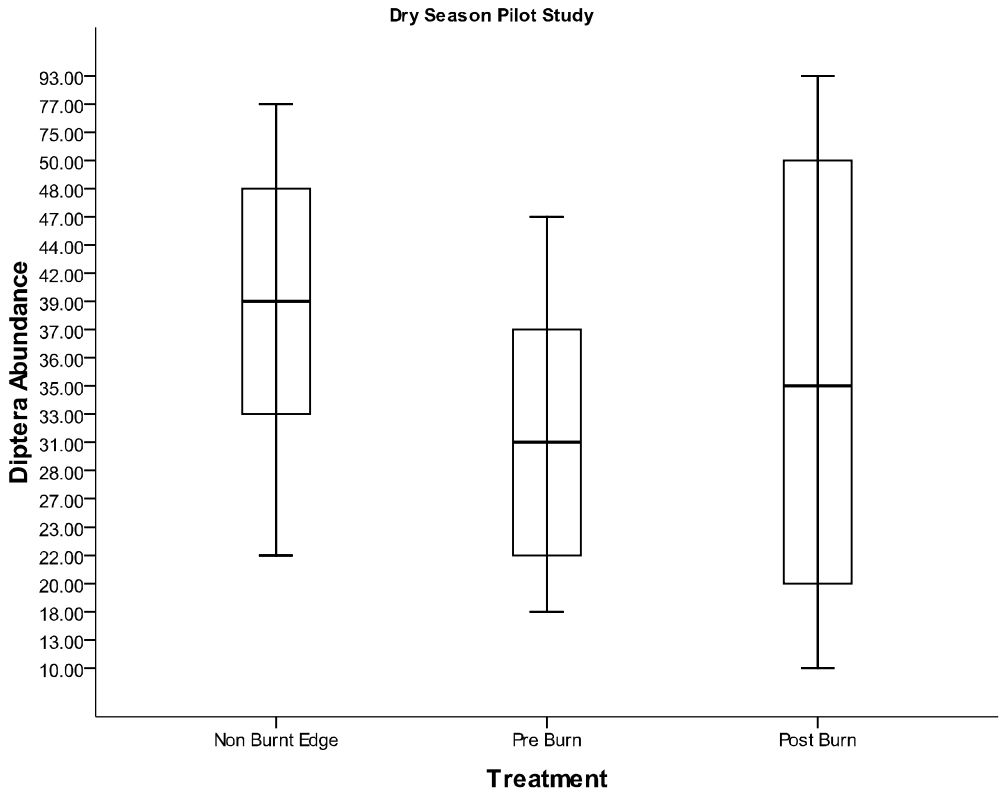
Distance and height data were organised into groups, for height; ground canopy (0 m above the forest floor), mid canopy (between 8 and 16 m above the forest floor) and high canopy (above 20 m from the forest floor). The height of the high canopy sample represents the highest that could be safely climbed within each tree and in general was < 10 m from the canopy crown. Horizontal distance subgroups were 5-10, 11-15, 16-25, 26-40, 41-60 and 61-80 m from the edge of the forest. All samples taken from > 100 m into the forest were classed as internal control plots. Grouping the data into these categories

allowed a certain level of data smoothing due to the averaging within each group. Later sections and chapters will look at specific distances and heights through regression analysis where smoothing is not necessary.

3.3.2.3 Results

3.3.2.3.1Pilot study of surrounding Savannah Matrix

The results of the Kruskal-Wallis test showed that in the dry season there was no significant differences in dipteran abundances between the non burnt or pre burnt savannahs or between pre burn and post burn abundances, $H = 2.163$, $df = 2$, $p = 0.339$. There was also no significant difference between the non burnt and post burnt savannah sites in the wet season, roughly four months after the burn (see fig. 3.9, below).



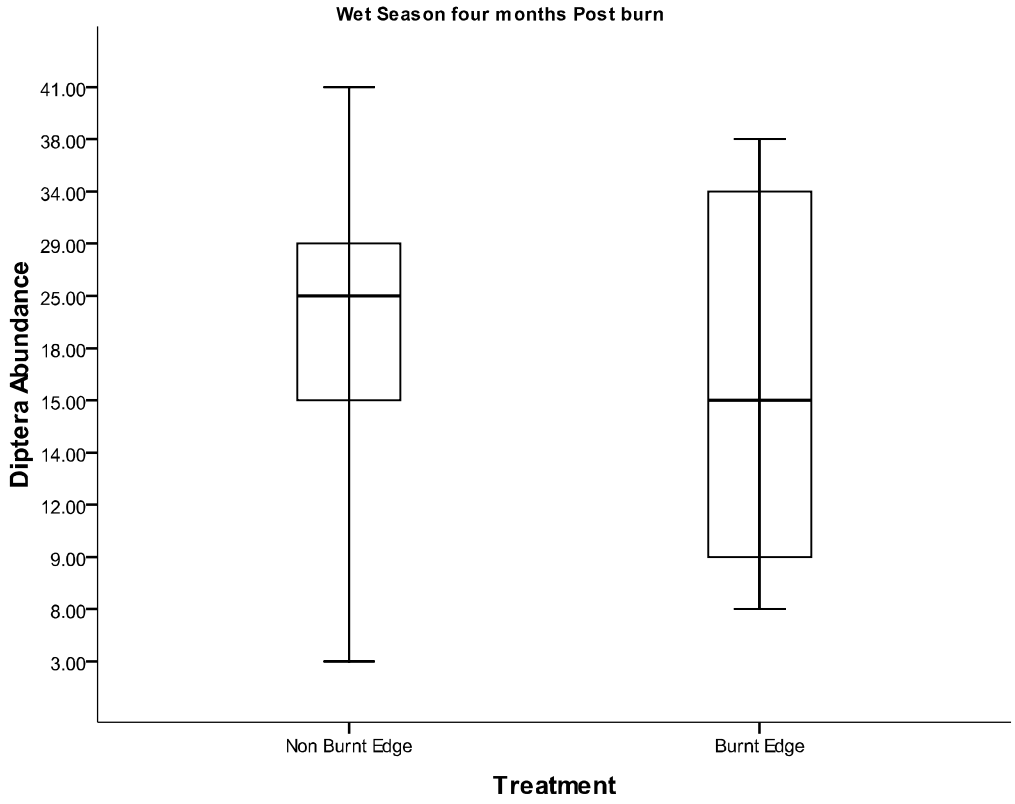


Fig 3.9. Dipteran abundance (per trap day) in pre burnt, post burnt and non burnt savannah plots in dry (top) and wet (bottom) seasons for Kwano savannah.

The final test that needed to be performed was between seasons to see if there was a marked effect four months after the burn. As the data were normally distributed a two way ANOVA was used to analyse the effect of both treatment and season. The results of the two way ANOVA showed that there was an overall difference within the model, and that seasonality had a specific effect within that model, F (1, 4) = 7.198, $p<0.05$, but treatment did not, F (3, 4) = 0.934, *ns*. There was no significant interaction between seasonality and treatment.

Post hoc analysis within the model for seasonality was not possible therefore a paired t-test was used to look for the specific difference. The pre burn savannah samples were withdrawn from the analysis so that group size was even. The results show that there was a significant difference between the wet and dry season samples, t = 7.718, df = 29, $p<0.001$, when both burnt and non burnt samples are pooled. To look for significant differences

between the treatments a Mann-Whitney U test was used as the sample size was much smaller. There was a significant difference between the wet and dry season non burnt edges, with dry season diptera abundance significantly higher, $U = 8$, $p < 0.05$, however there was no significant difference between burnt edge samples in the wet and dry season, $U = 12$, *ns*. In both the burnt and non burnt edges the dry season dipteran abundance was ranked higher than wet season abundance, however with the dry season burnt edge abundance ranked lower than the non burnt dry season abundance, no significant difference was shown between seasons in the burnt savannah (see fig 3.10, below).

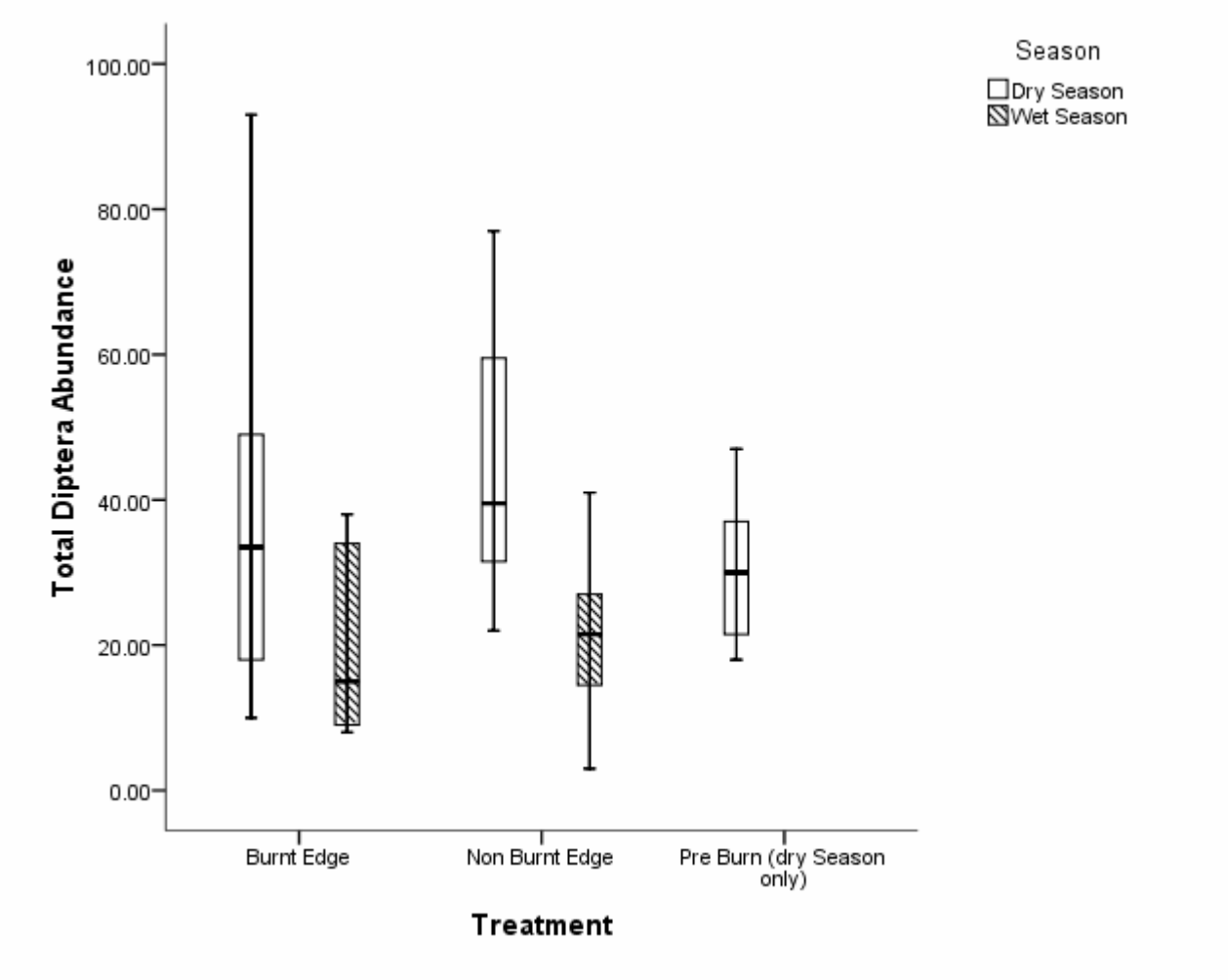


Fig 3.10. Between season differences in burnt and non burnt savannah Diptera abundance (per trap day), Kwano savannah.

3.3.2.3.2 Spatial Analysis

As the dipteran abundance data were not normally distributed they were transformed using an ln(x)+1 transformation before analysis. The spatial factors were explored using a multi factor ANOVA using distance of the sample from the edge, height within the canopy, and treatment as factors. The resulting model proved to be significant, F (12, 33) = 1.704, p < 0.05, with wet and dry season samples grouped together. There were no significant interactions within the model; however, post hoc analysis showed there to be significant differences within factors.

Post hoc analysis for distance was conducted with Hochbergs GT2 test as samples sizes varied. Samples from varying heights, treatments and season were pooled for this analysis. There was shown to be significant differences between the internal control plot and samples from 5-10 m from the edge ($p<0.05$), 11-16 m ($p<0.001$) and 41-60 m ($p<0.05$). There were no significant differences between all other groups. Fig 3.11 below illustrates the grouped distance data.

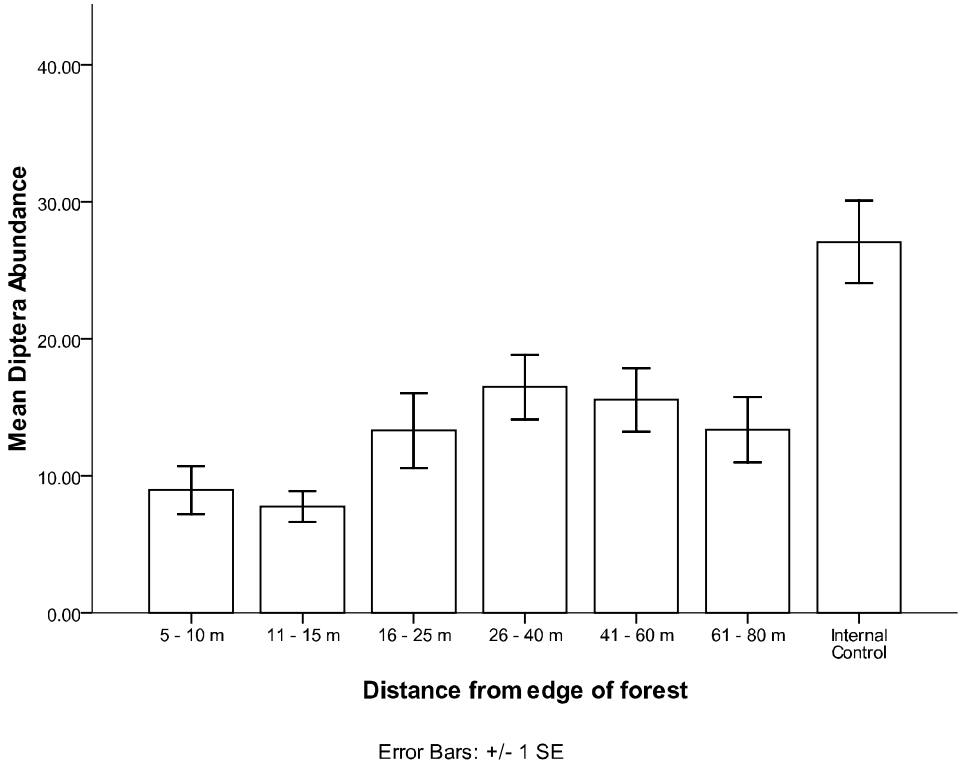


Fig. 3.11. Grouped dipteran abundance (per trap day) within distance categories, Kwano forest.

For treatment post hoc analysis Gabriel's procedure was used as group sizes only varied slightly. Again the results from other factors were pooled for this initial analysis. The post hoc analysis showed there to be a significant difference between Diptera abundance in the internal control plots and the non burnt edges ($p<0.001$) and the burnt edges ($p<0.001$), however there was no significant difference between the burnt edge and non burnt edge ($p>0.05$). Fig 3.12 below illustrates the differences between treatment groups.

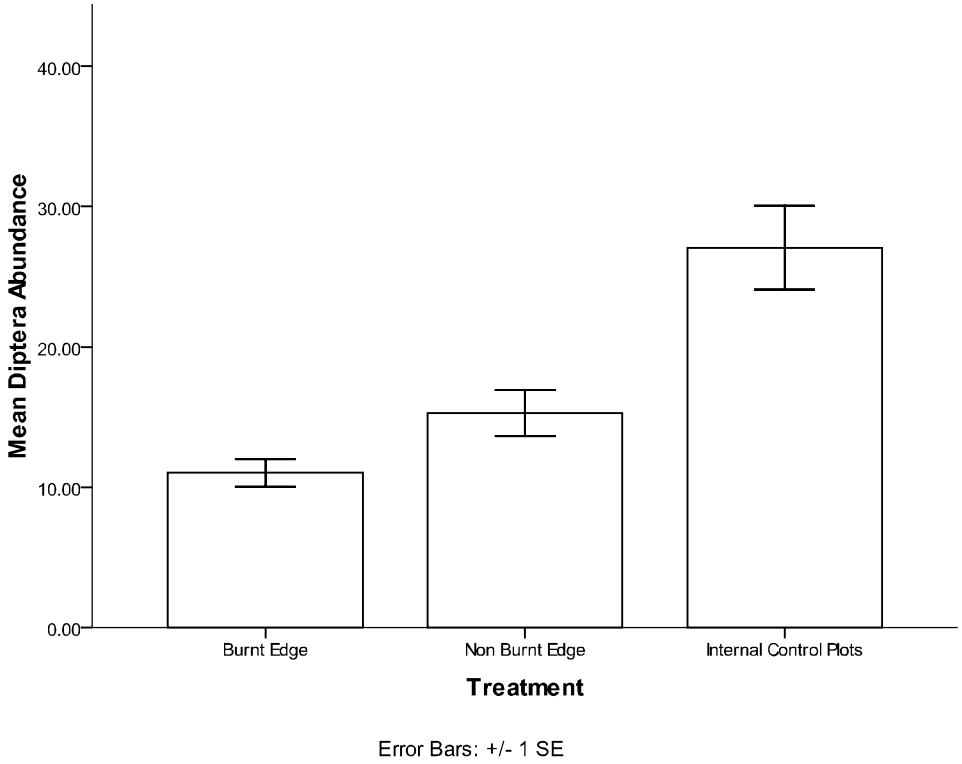


Fig. 3.12. Differences in Diptera abundance (per trap day) across all treatments, Kwano forest.

Height was the final factor to undergo post hoc analysis. As with the treatment factor a Gabriel's procedure was used as group sizes were slightly uneven. There were no significant differences within this factor at this scale (see fig. 3.13 below).

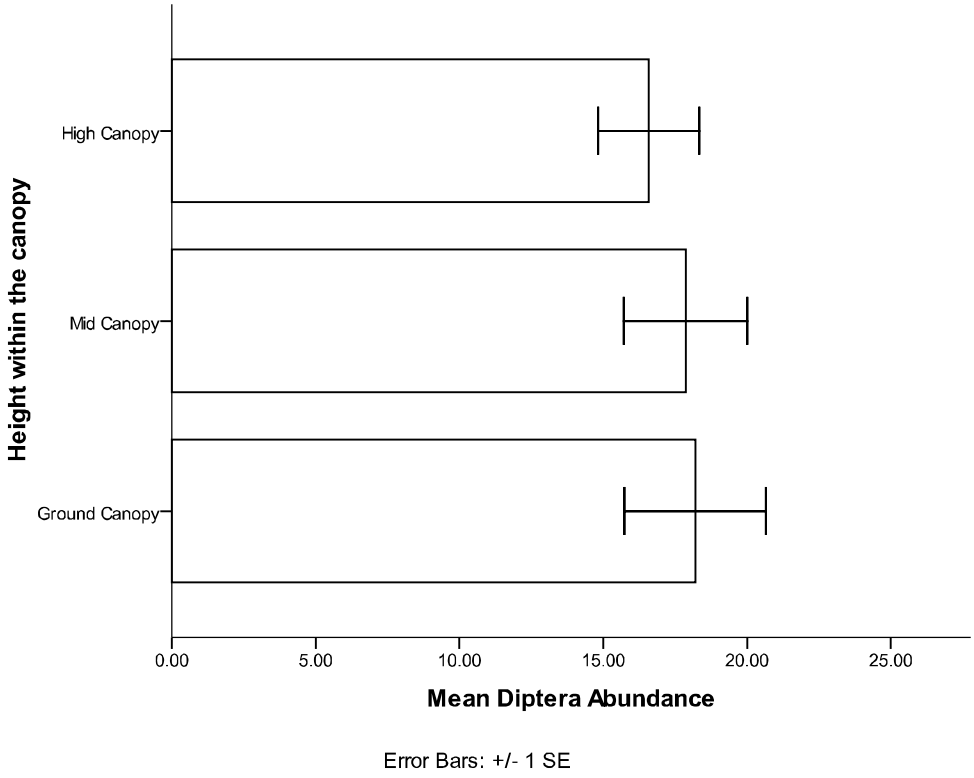


Fig. 3.13. Differences in dipteran abundance (per trap day) across all heights, Kwano forest.

In order to analyse these data at a finer scale, data were split by season and the analysis rerun, specifically targeting the effect of these factors within each of the seasons. The dry season multi factor ANOVA model proved to be highly significant, F (10, 119) = 3.03, p < 0.05. There were no significant interactions between factors but height showed significant differences within the group, F (2, 119) = 10.05 p < 0.05.

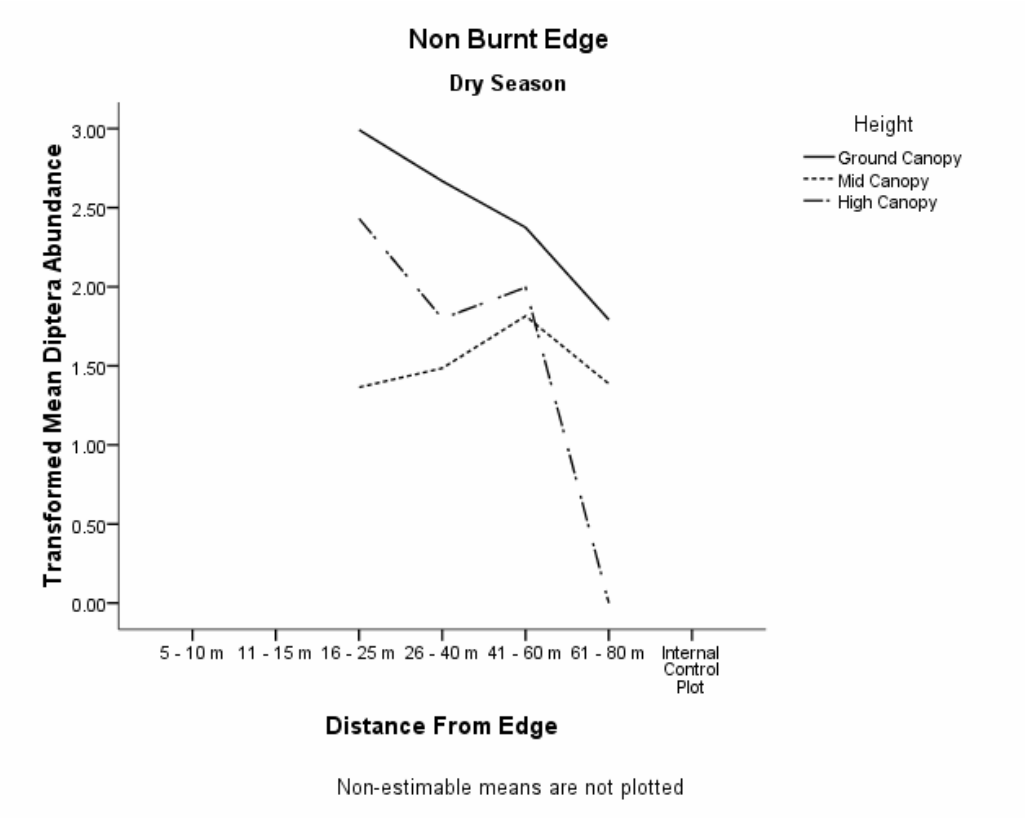


Fig. 3.14, Dipteran abundance (per trap day) at the burnt edge during the dry season, Kwano forest. Note: These and subsequent line graphs are used as a visual aid, not as a predictive model

Fig. 3.15, Dipteran abundance (per trap day) at the non burnt edge during the dry season, Kwano forest.

Grouped distance post hoc analysis was again conducted using Hochburgs GT2 test and as with the analysis at a higher scale the internal control plot was significantly different to all other distances from the edge, ($p<0.05$ for all distances from the edge), see figs 3.14 and 3.15 above.

Post hoc analysis of dry season height differences in height groups was conducted using Gabriel's procedure and the results show that there were significant differences between the ground canopy samples and mid canopy samples ($p < 0.05$) and the ground canopy and high canopy samples ($p < 0.05$), but there is no significant difference between mid and high canopy samples ($p > 0.05$), see fig 3.16 below.

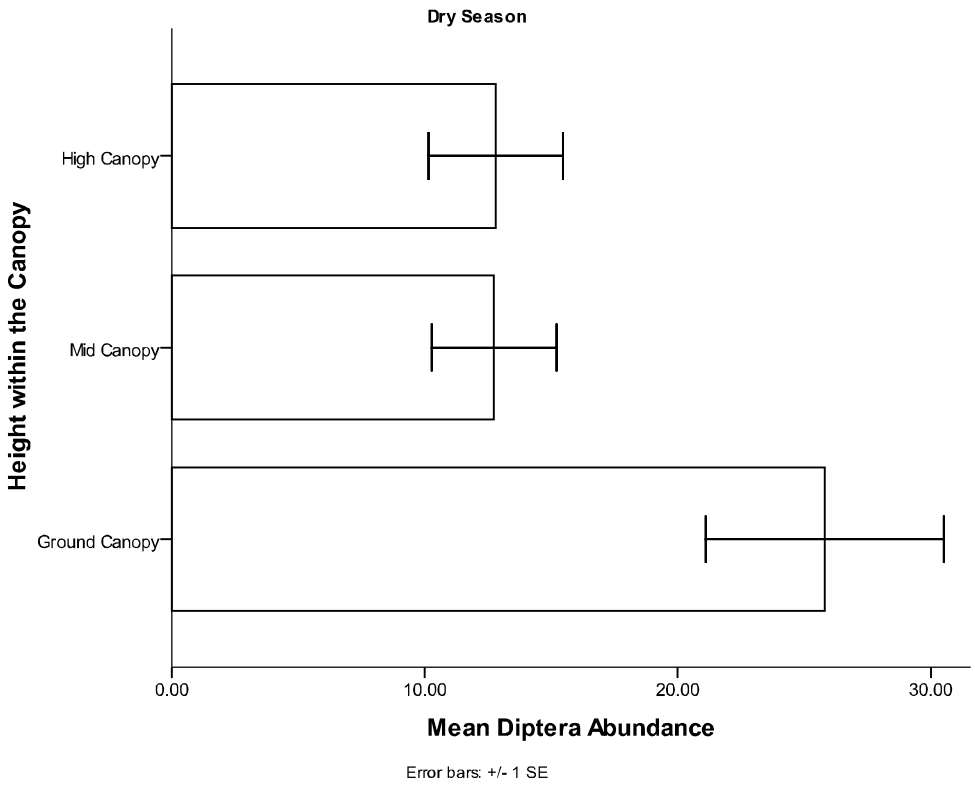


Fig 3.16. Dipteran abundance (per trap day) in different height classes within the dry season, Kwano forest.

The Gabriel's procedure also showed significant differences between grouped treatment data, with the internal control plots being significantly different to both burnt edge samples

($p<0.001$) and non burnt samples ($p<0.001$). However there was no significant difference between burnt and non burnt edges ($p>0.01$), see fig 3.17 below.

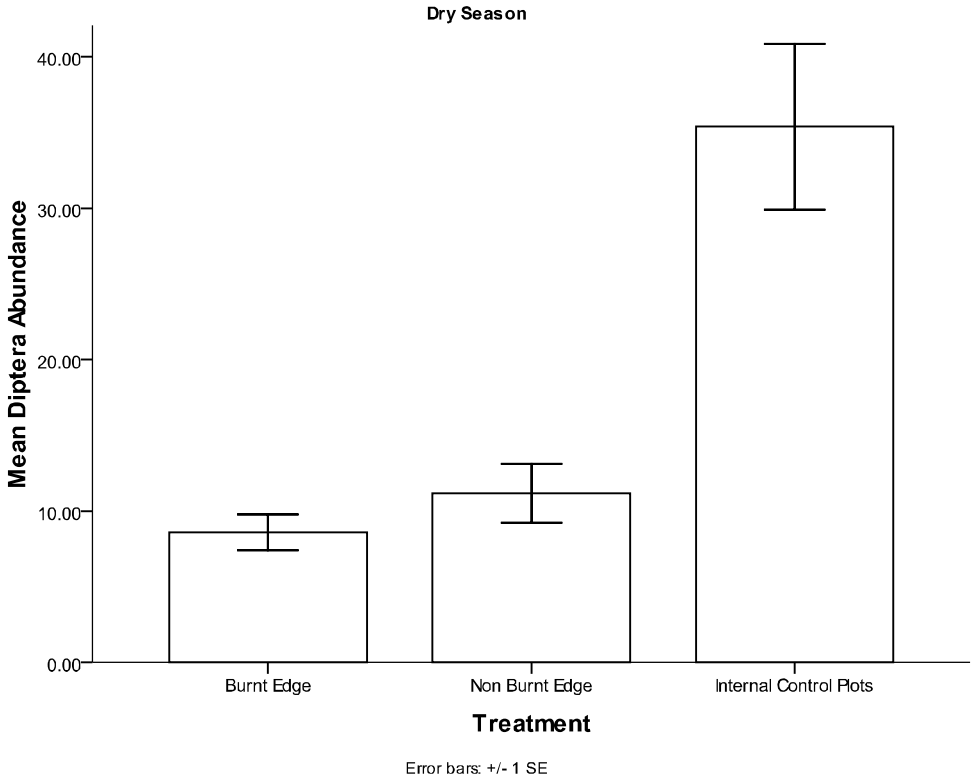


Fig 3.17. Dry season dipteran abundance (per trap day) across different treatment groups, Kwano forest.

The wet season ANOVA model showed no significance, F (12, 32) = 0.859, *ns*, and there were no significant interactions between or within factors.

Fig 3.18. Variation of dipteran abundance (per trap day) from the burnt edge of the forest in the wet season, Kwano forest.

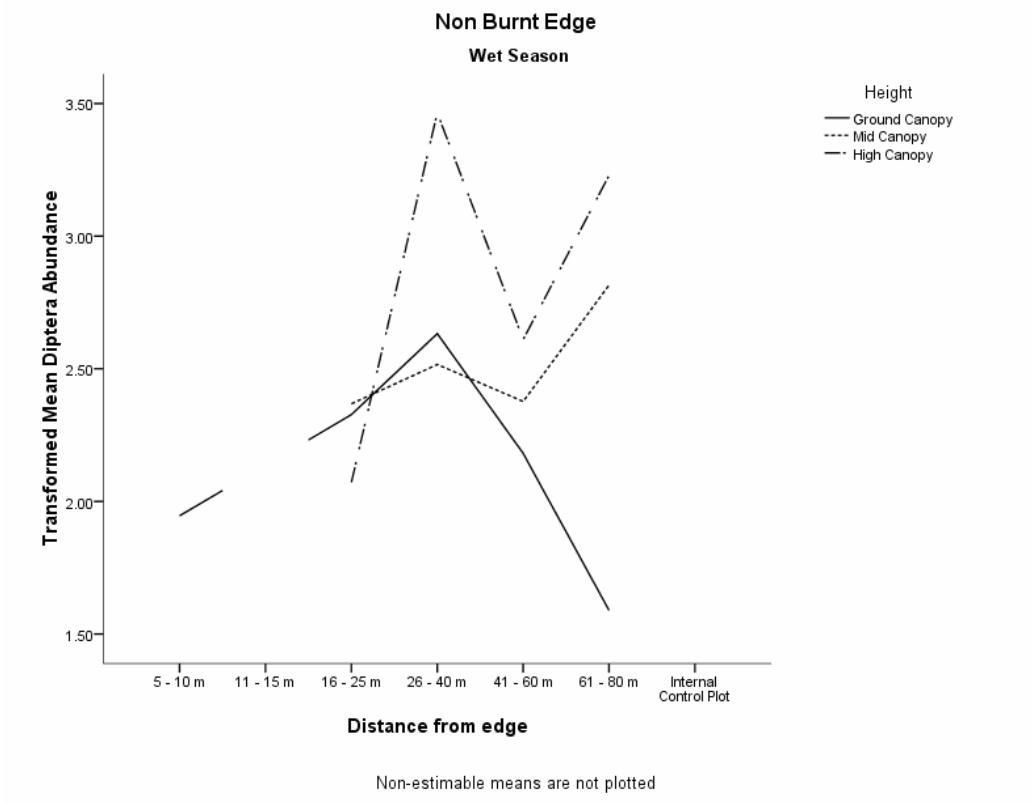


Fig 3.19. Variation of dipteran abundance (per trap day) from the non burnt edge of the forest in the wet season, Kwano forest.

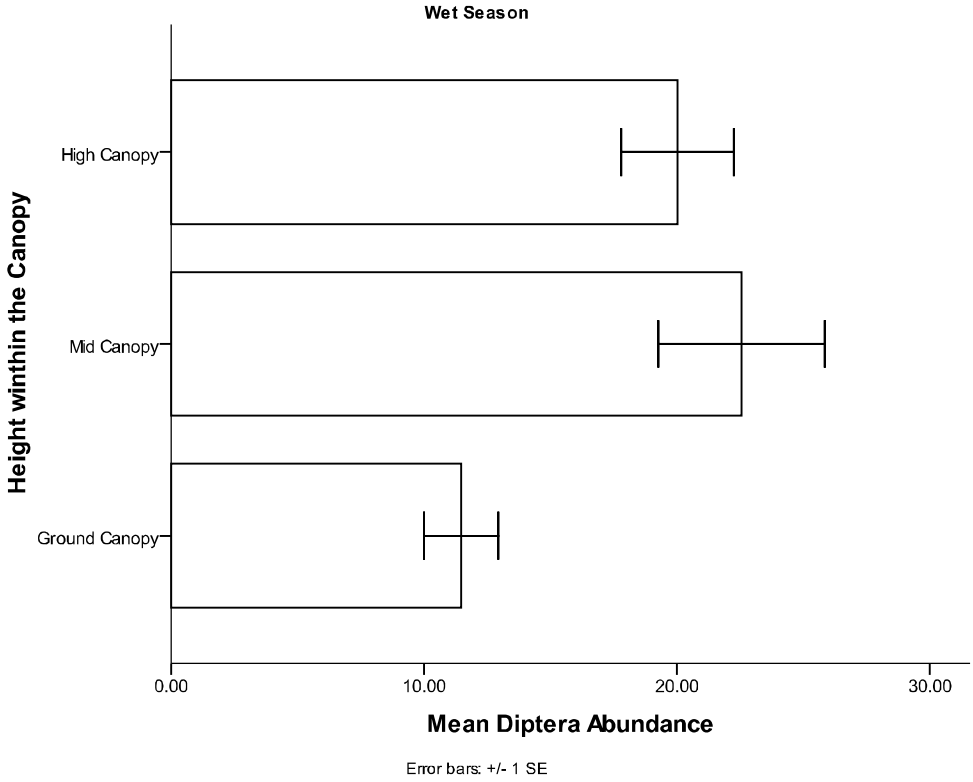


Fig 3.20. Variation of diptera abundance (per trap day) through the vertical column in the wet season, Kwano forest.

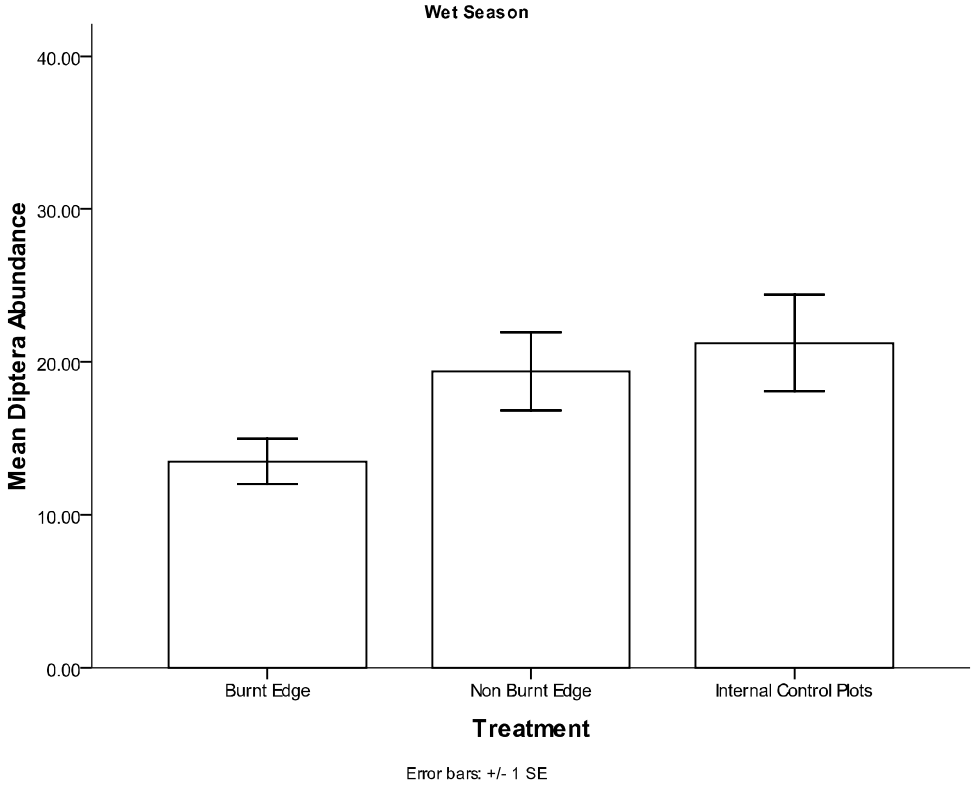


Fig 3.21. Differences in dipteran abundance (per trap day) in different treatment areas in the wet season, Kwano forest.

3.3.2.4 Diptera Ordinal Analysis Conclusions

The savannah matrix

The analysis of overall dipteran abundances showed that there was no difference between the two areas before the treatment burn; therefore we can assume that any further effects seen within the results are as a consequence of the treatment that each of the areas received. In chapter 1, burning of savannah was shown to be a practice that is widespread and has been conducted for thousands of years and therefore presumably beneficial to the indigenous population. The results from the savannah investigation here show that there is no overall difference in the abundance of Diptera between areas of savannah that have been burnt and areas that have not. This is not to say that the burning does not affect the community of Diptera but further investigation into the detailed community structure and diversity is needed.

Seasonality was shown to have an effect on the abundance of Diptera within the savannah matrix. Dry season samples showed higher abundances of Diptera, with significant seasonal differences at the dry and wet season non burnt edges, but no seasonal effect at the burnt edge. However with overall abundance higher in the dry season having no significant difference between the dry and wet burnt edge samples means that there is an effect of burning. The results suggest that burning is acting to maintain the abundance of Diptera within the wet season above the level that it might have been without the burn.

Burning the savannah would create re-growth during the late dry and early wet season. The presence of new growth vegetation allows gall forming Diptera to parasitize leaves in great numbers (Boukili et al., 2007). The Cecidomyiidae (a gall forming dipteran family)

were the dominant family sampled in the savannah (see section 5.3.1 for details), therefore their abundance could be bolstered by such activities.

Spatial analysis

This initial analysis has been conducted at a low level of resolution, pooling together data sets to ascertain if there are broad effects to be found. Yet even here there were significant trends showing through. The internal control plots showed a significantly higher dipteran abundance than samples taken between 5 and 15 m from the edge and between 41 and 60 m from the edge. This is somewhat against the general trend in previous research which found that populations at the edge tended to be higher due to marginal habitats encouraging a greater number of generalist species (Didham, 1997) Yet these results show that abundance is in fact much higher in the undisturbed forest. However as stated previously these data have been analysed at a low level of resolution and there may in fact be a very different story when analysing the community structure and abundance of Diptera families within different seasons and treatment areas.

Whereas in the savannah, treatment only had a seasonal effect, here in the forest we can see that there is an effect across both seasons. The internal control plots had a significantly higher abundance of Diptera than both the burnt and non burnt edges, but there is no significant difference between burnt and non burnt forest samples.

The third spatial element to be analysed was height within the canopy, here, when pooling season and distance data together there was no overall significant difference between the height classes. However as was shown with the Collembola in the previous section

seasonality can have a significant effect on the abundance on invertebrates. Therefore it is necessary to account for this.

Once seasonality is taken into account we can see more significant differences between the abundance of Diptera under certain conditions. Firstly there are significant differences between height classes within each of the seasons (fig 3.16 and 3.20). In the dry season the ground canopy has significantly higher dipteran abundance than both the mid and high canopy, whereas in the wet season, the abundance of the high canopy is significantly higher than the ground canopy. This would account for the lack of significance when the seasonal data are pooled, as the higher abundance shifts from ground to the high canopy during the wet season. The effects of height within the canopy will be explored in later chapters as there does appear to be significant differences in relative abundances, and using a finer resolution (eg family level richness and abundance) may enable us to determine the key factors behind this shift.

The significantly higher abundance of Diptera in the internal control plots seems to be a result of much higher abundance in the dry season, as within the wet season there is no discernable difference between each of the treatment factors.

These results show (demonstrate) that there is a significant change in dipteran abundance between the wet and dry season. These findings are in agreement with previous studies which have shown this (Breidenbaugh et al., 2009, de Araujo and dos Santos, 2009, dos Santos et al., 2010) . However here we can break down the data into its constituent spatial parameters and see how the patterns shift within this. Further chapters in this thesis will take these initial results and move them further on, introducing the effects of environmental factors, such as temperature, humidity and rainfall in to the analysis. This is necessary because here we have assumed that factors such as height within the canopy and

distance from the edge represent a linear progression from edge to interior or from ground to the canopy crown. However non plantation forests are not uniform, in fact they have a heterogeneous structure where canopy gaps, clearings, rivers, slope and aspect can affect the forest structure and therefore the micro climates and micro habitats within the canopy, which will in turn affect the community of Diptera present.

3.3.3 Detection of edge effects

3.3.3.1 Introduction

This section aims to detect underlying edge effects in Diptera abundance and environmental factors within the forest edges. In the previous section the distance data were pooled into groups in order to smooth the data for ANOVA analysis. However in this chapter the distance data will be analysed as they stand. Ewers & Didham (2006) proposed a tool kit of regression models with which to assess edge effects. The models they suggest are linear, power, logarithmic and unimodal in their construction. The advantage of using regression analysis for detecting edge effects is that variation of dependent factors within the data set is accounted for. However the main advantage of this particular set of regression models is that the more complicated models (power, logarithmic and unimodal) can be used to ascertain information other than just the mere presence of an edge effect. Through differentiation to the 1^{st} and 2^{nd} orders, the mid point, penetration and magnitude of any effects that are present can be determined. These are important factors as they can then be statistically compared in later chapters when investigating more specific aspects of the data set.

Another important aspect of using these models is that many authors have suggested that the edge effect is not just a phenomenon seen inside of the forest boundary (Ries et al., 2004, Didham, 1997, Ewers and Didham, 2006), but there is also an effect that extends into the adjacent habitat, in this case a savannah matrix. Therefore as the savannah Diptera data can be introduced to both the logarithmic and unimodal models to determine the extent of the effect across the boundary rather than just inside of the forest.

At this point is necessary to prove the methodology, show that these data can stand up to this type of analysis and determine what factors are important in terms of detecting edge effects. These initial results can then be taken forward into later chapters to determine finer scale patterns.

3.3.3.2 Methodology

Using models suggested by Ewers & Didham (2006) and procedures used by Shaw et al. (2007) this section will establish if there is a baseline edge effect within this tropical Nigerian forest. Data will be analysed split between height within the canopy and season. The dependent data used within each of the models are maximum and minimum temperature and humidity, transformed total distance to nearest vegetation and transformed Diptera abundance (dipteran abundance was transformed according to the model being used). Distances from the edge of the forest were measured by tape for edge transects (<100 m from edge) or by estimation from GPS data for internal control plots (>100 m from the edge). Unlike the previous section the savannah data were added to the forest data for the logarithmic and unimodal models as these models can show how the data can be modelled across the boundary.

Before regression analysis is conducted it is important to establish if there are correlations between distance from the edge of the forest and the factors analysed here. Pearson's correlations were conducted in the first instance, and as the Diptera abundance was not normally distributed it was transformed with a Ln + 1 transformation. Following this a simple linear regression was conducted before the more advanced models. For non linear regression analysis a Spearman's correlation was performed prior to analysis as the results don't need to detect a linear relationship but to a monotone trend, sharing continued gradual/incremental changes with distance to edge. The non linear models were constructed in SPSS 17, using the nonlinear model function. Each equation was built based on the equations proposed in Ewers & Didham's (2006) paper, and took the forms:

$$F(x) = B_0 + (B_1 - B_0)e^{-B_2 x}$$ Power model

Where B_0 is the y intercept at x = 0, B_1 is the value of y at asymptote, B_2 is the positive scaling factor, and F(x) is the value of y at x.

$$F(x) = B_0 + \frac{B_1 - B_0}{1 + e^{(B_2 - x)B_3}}$$ Logarithmic model

Where B_3 is an additional scaling constant.

$$F(x) = B_0 + \frac{(B_1 - B_0)}{1 + e^{(B_2 - x + B_4 x^2)B_3}}$$ Unimodal modal

Where B_4 is an additional scaling constant and there is an additional x^2 term.

The power model equation shown here was adapted by Shaw et al. (2007) from Ewers & Didham's original paper; however the two remaining model equations are as they appear in their paper. In order to ascertain the midpoints, magnitude and penetration of the edge effect further mathematical investigation is needed. The power model contains the ability to discover the midpoint of the effect through the relationship $D_{1/2} = Ln(2)/B_2$ (where D is the distance from the edge (*x*)). However no other information can be derived from this particular model. The logarithmic and unimodal models can yield further information regarding the magnitude and penetration of the effect by using the 1st and 2nd derivatives. Ewers & Didham (2006) go through this relationship in some detail so it will not be repeated here.

Using the power model the magnitude and extent of the effect can be calculated from either the equation as it stands (magnitude) or from the first and second derivatives of the equation (extent) (Ewers and Didham, 2006). The magnitude is simply calculated by solving the numerator of the equation ($B_1 - B_0$) and the extent by the producing graphs of the first and second derivatives which reveal either maxima or minima which denote the distance from the edge where the change in the response function is at its greatest, which represents the midpoint of the edge effect (1st derivative) or local maxima and minima show the distance of penetration of the edge effect (2nd derivative). The equation of the first derivative takes the form;

$$\frac{d}{dx} = -\frac{(B_1 - B_0)e^{(B_2 - x)B_3} B_3}{\left[1 + e^{(B_2 - x)B_3}\right]^2}$$

and the equation of the second derivative takes the form;

$$\frac{d^2}{dx^2} = -\left[\frac{(B_1 - B_0)\omega B_3^2}{(1+\omega)^2} - \frac{2(B_1 - B_0)\omega^2 B_3^2}{(1+\omega)^3}\right]$$

Where; $\omega = e^{(B_2 - x)B_3}$

As with the logarithmic model magnitude and extent of the effect can be calculated from the original equation and the again the 1st and 2nd derivatives of the unimodal equation, which take the forms;

$$\frac{d}{dx} = -\frac{(B_1 - B_0)e^{(B_2 - x + B_4 x^2)B_3} B_3 (2xB_4 - 1)}{\left[1 + e^{(B_2 - x + B_4 x^2)B_3}\right]^2}$$

and

$$\frac{d^2}{dx^2} = -\left[\frac{(B_1 - B_0)\delta\theta^2 + 2(B_1 - B_0)\delta B_3 B_4}{(1+\delta)^2} - \frac{2(B_1 - B_0)\delta^2\theta^2}{(1+\delta)^3}\right]$$

Where $\delta = e^{(B_2 - x + B_4 x^2)B_3}$, and $\theta = (2xB_4 x - 1)B_3$.

Unlike the logarithmic model we cannot simply solve the numerator of the equation to find the magnitude; here the minimum value is the smaller of (B_1-B_0) and maximum is calculated by solving the original equation for F(x) where x takes the value at the central inflection point on the first derivative curve. Plots of the 2nd derivative show the physical extent of the effect which is shown by the distances between the local maxima and minima of the curves

To evaluate how well each of these models performed in respect to each other the models were analysed using Akaike's Information Criteria (AIC). AIC can be calculated using either the likelihood of the model or by using the Residual Sum of Squares (RSS). Using SPSS 17 means that likelihood values are not calculated using the nonlinear regression function, therefore the RSS was used to assess these models. The formula to calculate the AIC takes the form;

$$AIC = n\ln\left(\frac{RSS}{n}\right) + 2K$$

Where n = the number of samples and K = the number of parameters in the equation (including an error term). However as many of these models use a data set that has a ratio of $n/K < 40$, a bias correction is needed, which takes the form;

$$AIC_c = n\ln\left(\frac{RSS}{n}\right) + 2K + \frac{2K(K+1)}{(n-K-1)}$$

The best model can then be calculated by subtracting the minimum AIC_c from the AIC_c of the target model within the family of models of each dependent factor this is known as Δ_i, the likelihood of the model is calculated by the exponential of this figure, $e^{(-0.5\Delta i)}$, and finally the Akaike weight can be calculated by using the sum of all the likelihoods within the family of models for each dependent factor by using the equation;

$$w_i = \frac{e^{-0.5\Delta_1}}{\sum_{r=1}^{R} e^{-0.5\Delta_1}}$$

All non linear models were built using the non linear function in SPSS 17. This function requires a starting point for all constants within the equation, and these starting points need to be as close to the actual constants as possible, otherwise the regression analysis output

results in unrealistic constants with standard errors several orders of magnitude greater than the constants themselves. This was done by drawing on points from the dataset and solving each equation for the constituent part that was needed. In general as long as each constant was in the right order of magnitude the non linear function can accurately predict possible constant values (see Royall (1997) and Burnham and Anderson (2002) for details of AIC calculation).

3.3.3.3 Results

3.3.3.3.1 Linear and Power models

Pearson's correlations were used to establish if there were correlations between the distance from the edge of the forest and the dependent factors, Table 3.2, below, shows the results of this analysis.

Table 3.2, Pearson's correlations and linear regression results for distance against transformed Diptera abundance and all environmental factors; residual normality, mean and pattern information are also displayed.

Dependent	Season	Height	R	R^2	Normality	Mean	Pattern
Max temperature ºC	Dry	Ground	-0.351	0.123	Yes	0	No
		Canopy					
		Mid Canopy	-0.245	0.060	Yes	0	No
		High Canopy	-0.294	0.087	Yes	0	No
	Wet	Ground	0.247	0.075	Yes	0	No
		Canopy					
		Mid	0.238	0.057	Yes	0	No

		Canopy					
		High Canopy	0.456*	0.208*	Yes	0	No
Min Temperature ºC	Dry	Ground Canopy	0.569*	0.323*	Yes	0	No
		Mid Canopy	0.515*	0.266*	Yes	0	No
		High Canopy	0.338	0.114	Yes	0	No
	Wet	Ground Canopy	-0.306	0.093	Yes	0	Yes
		Mid Canopy	-0.263	0.069	Yes	0	Yes
		High Canopy	-0.347	0.120	Yes	0	Yes
Max Humidity %RH	Dry	Ground Canopy	0.689**	0.446**	Yes	0	Yes
		Mid Canopy	0.786**	0.618**	Yes	0	Yes
		High Canopy	0.808**	0.634**	Yes	0	Yes
	Wet[$]	Ground Canopy	NA	NA	-	-	-
		Mid	NA	NA	-	-	-

		Canopy					
		High Canopy	0.219	0.048	No	0	Yes
Min Humidity %RH	Dry	Ground Canopy	0.659**	0.434*	Yes	0	No
		Mid Canopy	0.775**	0.596**	Yes	0	No
		High Canopy	0.747**	0.558**	Yes	0	No
	Wet	Ground Canopy	-0.302	0.091	Yes	0	No
		Mid Canopy	-0.307	0.094	Yes	0	No
		High Canopy	-0.412	0.170	Yes	0	No
Transformed Diptera Abundance	Dry	Ground Canopy	0.541**	0.292**	Yes	0	No
		Mid Canopy	0.812**	0.476**	Yes	0	No
		High Canopy	0.662**	0.286**	Yes	0	No
	Wet	Ground Canopy	-0.004	0.009	Yes	0	No
		Mid	0.449*	0.035	Yes	0	No

		Canopy High Canopy	0.297	0.077	Yes	0	No
Log distance to nearest vegetation		Ground Canopy	0.248	0.062	Yes	0	Yes
		Mid Canopy	0.02	0.000	Yes	0	No
		High Canopy	0.511*	0.300	Yes	0	No

[$] Max Humidity was always 100 %RH therefore no correlation possible,

* Significant to $p<0.05$,

** Significant to $p<0.005$,

R Pearson's correlation coefficient

R^2 Linear Regression model fit,

- Regression not analysed

From the above table we can see that the best performing data are dry season maximum and minimum humidity and dry season Diptera abundance.

Simple linear regression was used to analyse the above environmental factors together with dipteran abundance using again distance from the edge of the forest as the independent factor. Once the linear regression had been run for each of the factors at each height and each season, their standardised residuals were analysed to make sure that no assumptions of the test had been violated. Residuals were analysed for normality through a one sample Kolmogorov-Smirnov test and plotted on a QQ plot, means were assessed to confirm that

they equalled zero and the residuals were plotted on a scatter plot to look for potential patterns. If a pattern was found within the residual scatter plot then linear regression assumptions were deemed to be violated. The results of the residuals analysis can be seen in the above table.

Analysis of the standardised residuals showed that of all the significant linear relationships only maximum humidity in the dry season violated the linear regression tests as a pattern appeared in the residual plots. Figures 3.22 – 3.24, below, show that although no discernable pattern is detectable at the edge of the forest, once the forest core has been reached there is a detectable pattern.

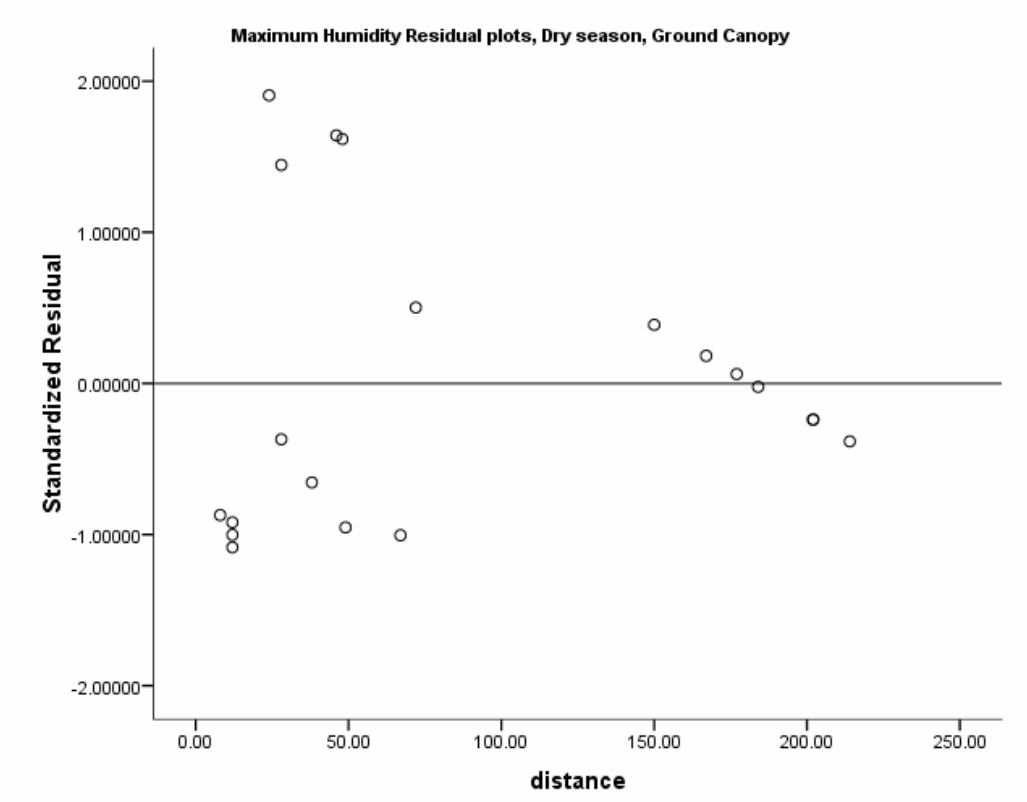


Fig 3.22. Maximum humidity (%RH) residual plots for the ground canopy in the dry season.

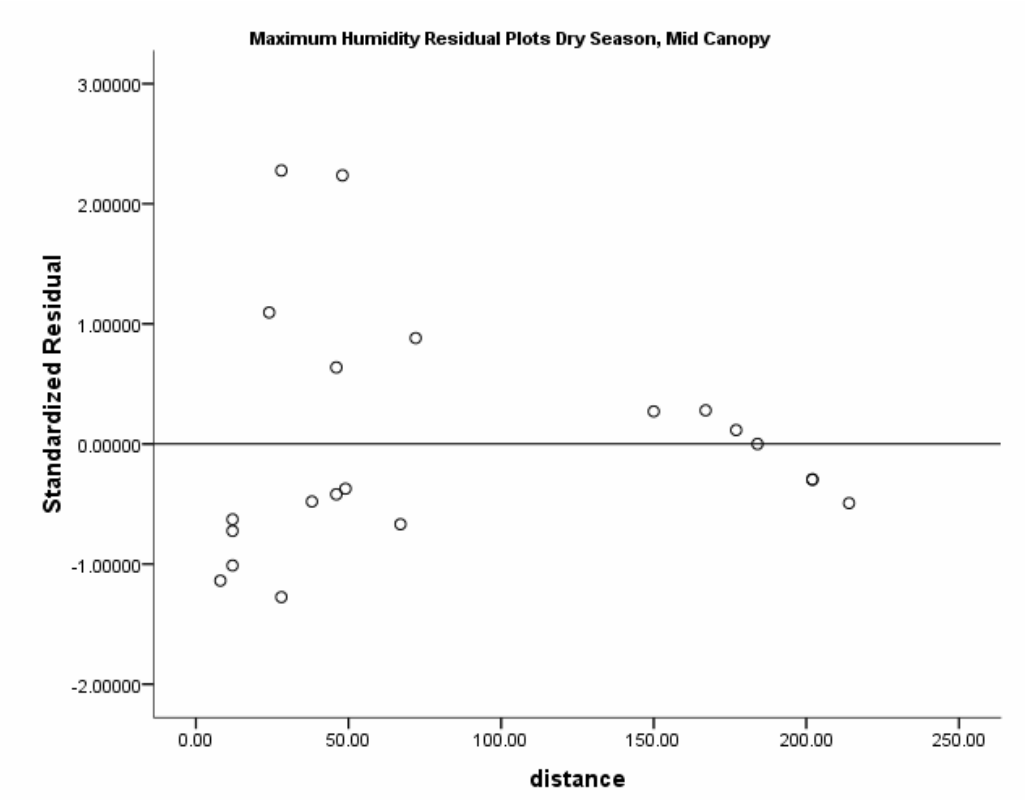


Fig 3.23. Maximum humidity (%RH) residual plots for the mid canopy in the dry season.

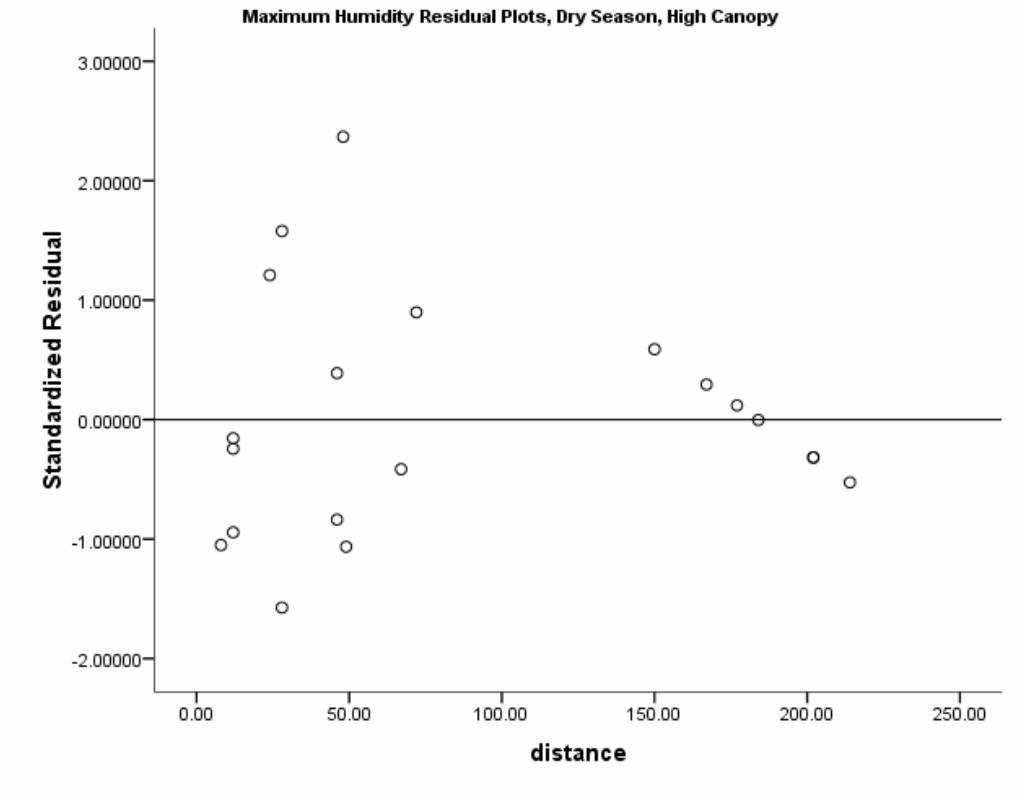


Fig 3.24. Maximum humidity (%RH) residual plots for the high canopy in the dry season.

With a detectable pattern in these data there is the opportunity to see if a higher level regression model will explain the relationship better, therefore a non linear power model was fitted.

The advantage of using this particular model is that although the model cannot tell us the magnitude or absolute extent of the edge effect it can predict the half distance ($D_{1/2}$) of the effect as B_2 is related to the half distance by the equation $D_{1/2} = \ln(2)/B_2$. Therefore once the power models were run the half distance ($D_{1/2}$) was then calculated from the constants (see table 3.3 below).

Table 3.3 Exponential fit, half distance of effect and residual analysis for the power model. Note: models that were not fitted or fitted too poorly were removed from these results.

Dependent	Season	Height	R_S	R^2	$D_{1/2}$	Normality	Mean	Pattern
Min Temperature ºC	Dry	Ground Canopy	0.589*	0.427**	25.67	Yes	0	No
		Mid Canopy	0.447*	0.274**	99.02	Yes	0	No
		High Canopy	0.328	0.128**	49.51	Yes	0	No
Max Humidity %RH	Dry	Ground Canopy	0.809**	0.558**	27.73	Yes	0	Yes
		Mid Canopy	0.852**	0.685**	40.77	Yes	0	Yes
		High Canopy	0.808**	0.694**	57.76	Yes	0	Yes

Min Humidity %RH	Dry	Ground Canopy	0.696**	[a]	-	-	-	-
		Mid Canopy	0.731**	0.599**	231.05	Yes	0	No
		High Canopy	0.609**	0.560**	346.57	Yes	0	No
Transformed Diptera Abundance	Dry	Ground Canopy	0.425*	[a]	-	-	-	-
		Mid Canopy	0.630**	0.483**	115.52	Yes	0	No
		High Canopy	0.452**	[a]	-	-	-	-
Log distance to nearest vegetation		Ground Canopy	-0.146	[a]	-	-	-	-
		Mid Canopy	-0.265	0.185*	4.252	Yes	0	No
		High Canopy	0.127	0.002*	3.629	Yes	0	No

* Significant to $p<0.05$,

** Significant to $p<0.005$,

- Regression not analysed

R_S Spearman's correlation coefficient

R^2 exponential fit from regression analysis

$D_{1/2}$ half distance of edge effect (m)

[a] data took too few values for exponential fit

With the exception of the minimum humidity, where the regression analysis returned results where the standard errors where probably outside the acceptable level ($B_2 = 0.003$,

SE = 0.009, B_1 = 11.760, *SE* = 7.495, B_0 = 105.993, *SE* = 239.913), the parameters performed well in the power model with the data returning half distance data that are more than reasonable and standard errors well within acceptable limits. Unstandardised residuals were checked for violations of assumptions, and again only maximum humidity data violated the assumption with the presents of patterns (similar to those from the linear regression residuals, see fig 3.23 – 3.24 above) within the residual plots.

Comparing the R^2 values of the linear and power models (tables 3.2 and 3.3 respectively) we can see that overall the power model produced a better fit than the linear model. There are still some residual violations so a further model will be fitted to the data, however this will be tested later using AIC and AIC weightings.

3.3.3.3.2 Logarithmic model

The next model is a logarithmic model which can compose of positive and negative *x* values. Ewers and Didham (2006) suggest that this form of model represents the relationship of the data from the savannah matrix across the forest edge and into the forest interior. Unfortunately no environmental data were taken outside the forest; however Diptera abundance data were collected in year one up to 30 m into the adjacent savannah. It is therefore these data that will be used to assess if the logarithmic model fits. So far the Diptera abundance data has not performed as well in the regression models as the environmental data, although it did perform slightly better in the power model (R^2 = 0.483, $p<0.001$) than the linear model (R^2 = 0.476, $p<0.001$).

With the addition of another scaling constant the likelihood of unstable/impossible standard errors (ether 0 or $>10 \times 10^{10}$) may be produced, as well as the number of iterations used by the programme reaching its maximum before constants have been found.

Therefore as well as analysing the residuals of each analysis, attention was also paid to these elements of the output. For example if the standard error was greater than twice the value of the constant then the model was not accepted, and accordingly if constants could not be found within the limit of iterations set by the analysis the model was not accepted.

As with the previous models, total dipteran abundance and environmental factors were considered as dependent factors and distance the independent factor. Because in some instances (namely the dipteran abundance) the values of *x* spread across zero, values of *x* outside of the forest were considered to be positive values and values of *x* inside the forest were considered negative values. For the environmental data, where there were no data taken outside of the forest *x* values were kept as negative for consistency.

Table 3.4. Logarithmic regression analysis results

Dependent factor	Season	Transect	B_0	B_1	B_2	B_3	R^2	Stable SE	Iteration limit met	Residu assum met
Transformed Diptera Abundance	Dry	Ground	1.83	1.34	-181.36	0.22	0.11	Yes	No	
		Mid	1.41	0.73	-83.64	0.04	0.46	Yes	No	
		High	1103	0.73	-837.40	0.01	0.31	No	No	
	Wet	Ground	1.29	1.04	-8.38	-12.9	0.16	No	No	
		Mid	1.52	0.95	-24.02	58.0	0.45	No	No	
		High	494	1.20	-582.01	0.22	0.09	No	No	
Minimum Temperature	Dry	Ground	21.2	-9166	279.74	0.03	0.43	No	Yes	Y
		Mid	21.4	18.54	-69.782	1.47	0.39	Yes	No	
		High	21.2	-3635	516.85	0.01	0.13	No	Yes	Y
	Wet	Ground	20.7	-77.39	-413.28	-0.03	0.14	No	Yes	
		Mid	53.3	11.82	-4.15	0.00	0.07	No	No	
		High	20.5	-429.6	-282.40	-2.67	0.24	No	Yes	

Minimum	Dry	Ground	120167	25.73	-453.99	0.03	0.46	No	No	Y
Humidity		Mid	51.00	18.77	-72.179	4.28	0.66	No	No	
		High	49.00	19.83	-72.25	3.84	0.62	No	No	
	Wet	Ground	83.28	65.50	-203.23	-2.51	0.22	No	No	
		Mid	68.83	59.11	-58.10	-0.28	0.18	Yes	Yes	Y
		High	64.30	-117192	-545.24	-0.03	0.26	No	No	Ye
Transformed	Dry and	Ground	1.28	1.50	-13.27	0.51	0.37	Yes	No	
Distance to	Wet	Mid	2.16	2.03	-72.39	3.98	0.04	No	No	
Vegitation		High	2.99	2.44	.177.51	2.94	0.52	No	No	

* Residual mean 0.0002

** Residual mean 0.0004

B_x Constants from the equation

R^2 Logarithmic fit

SE Standard error

The table 3.3 (above) shows the results of the logarithmic regression analysis, factors such as maximum humidity and maximum temperature were a poor fit to the model so the results are not shown here. At several points in the above table there are constants that seem to be impossible, for example where humidity maxima or minima are above 100 or below zero. This is the result of the model not being able to find a constant within the range of data collected; this simply means that either B_1 or B_0 fell outside of the values of x analysed within the model. These results often coincide with the limit of iterations also being exceeded, as the programme cannot find a stable constant. However even when the iteration limit was not exceeded, many of the results returned standard errors that were far too high to regard as a properly fitting model even if the R^2 was showing a seemingly good fit (>0.4). From all the data show in the above table only five independent variables performed well in the analysis, they are; dry season ground and mid canopy transformed dipteran abundance, dry mid canopy minimum temperature, wet season mid canopy

minimum humidity and dry season ground canopy distance to vegetation. Therefore these factors were taken to the next stage of deducing their midpoints, magnitude of effect and the physical extent of the effect (see table 3.4 below).

Table 3.4. Magnitude and extent of edge effects.

Dependent Factor	Season	Transect	$B_1 - B_0$ (magnitude)	Mid point of effect (m within forest)
Log10 diptera abundance	Dry	Ground canopy	-0.495	181 m
		Mid canopy	-0.68	84 m
Minimum Temperature (ºC)	Dry	Mid canopy	-2.843	70 m
Minimum Humidity (%RH)	Wet	Mid canopy	-9.722	58 m
Ln Distance to nearest vegetation (m)	Dry	Ground Canopy	0.221	13 m

To calculate a more accurate midpoint of the effect, the model was redrawn along an axis where *x* ranged from 30 to -300 (30, 29, 28, 27, ect). From the above table we can see that the midpoint of the effect is actually equal to B_2 in all cases, therefore rather than using the 1st derivative of the curve we can simply state that the midpoint of the effect is equal to B_2.

From fig 2.25, below, we can see how the 1st derivative curves perform. From them it can been seen that the models that have the smaller R^2 values (<0.40) show only a limited effect over a few 10's of meters. The one model that has an R^2 of over 0.40 (mid canopy

dry season dipteran abundance) has a much more realistic effect, with the range of the curve starting outside of the forest boundary.

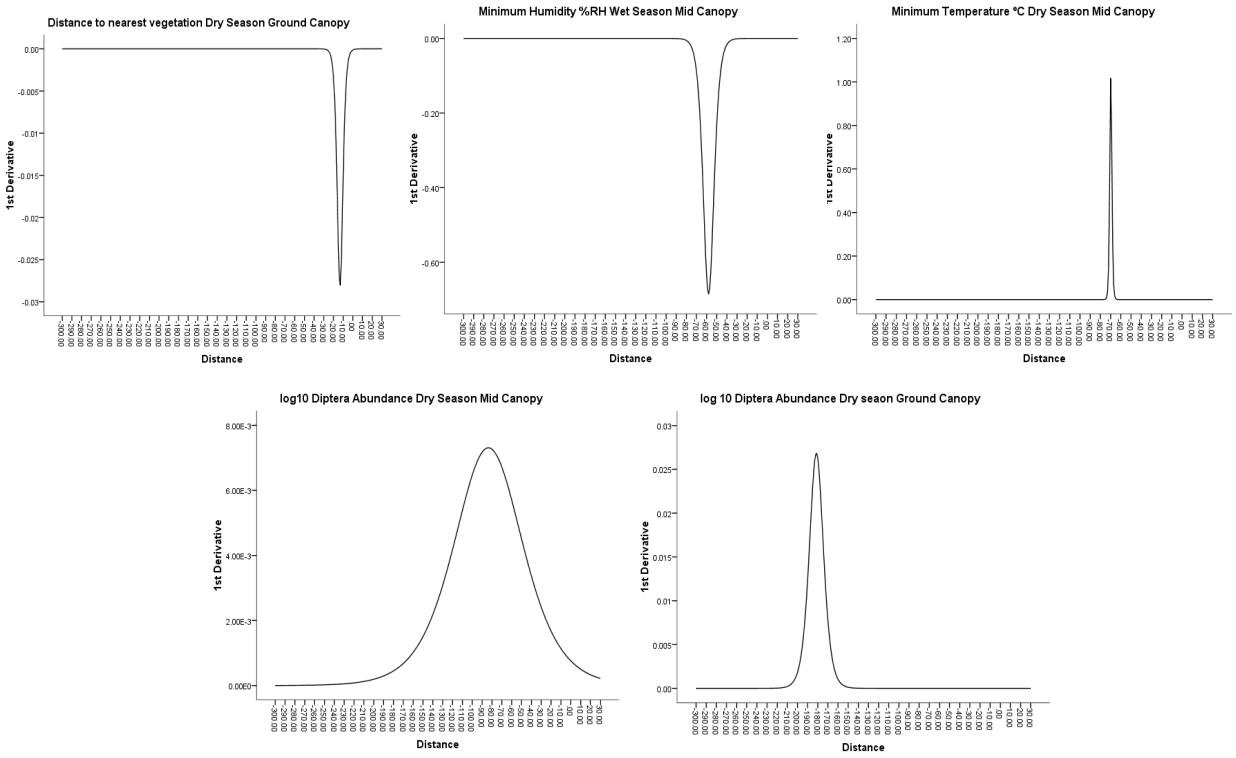


Figure 3.25. First derivative of the logarithmic model with a refitted x axis.

To further illustrate the performance of these models plots of the 2nd derivative were created. They show the physical extent of the effect which is shown by the distances between the local maxima and minima of the curves (Fig. 2.26, below).

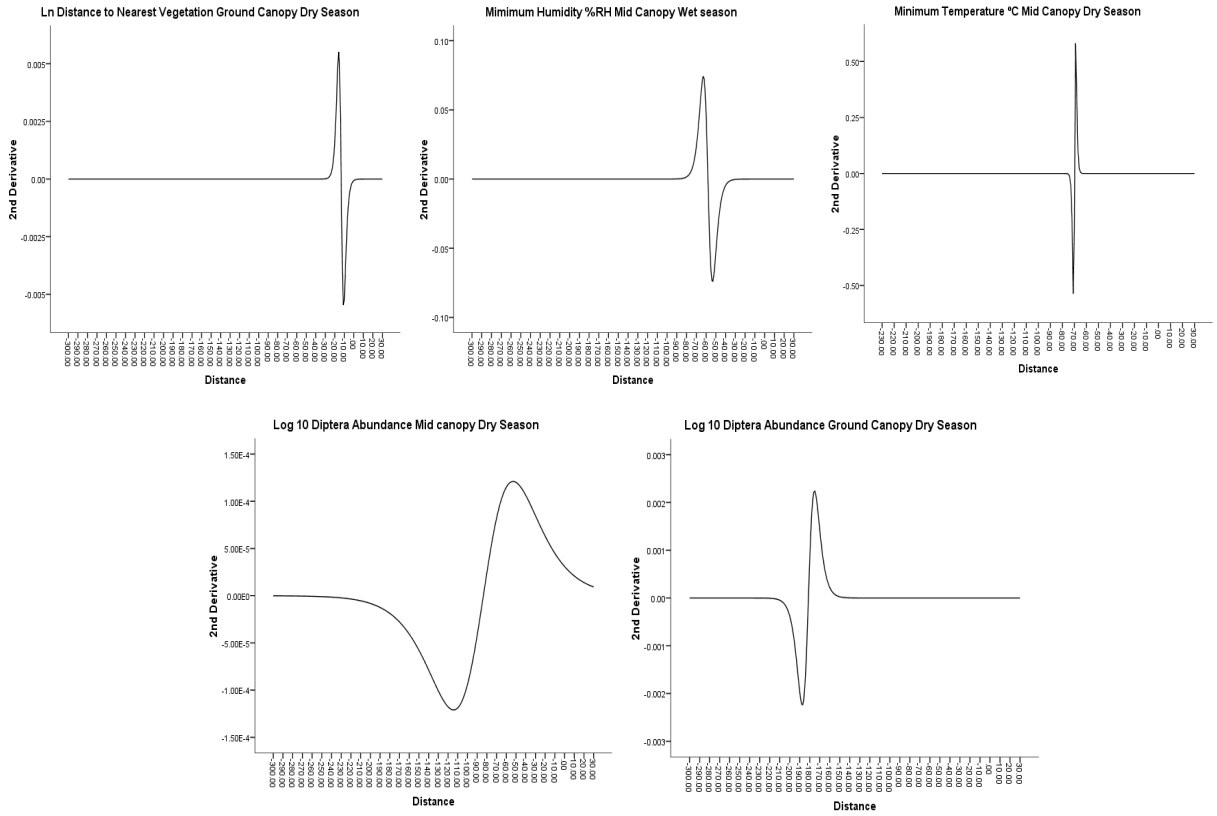


Fig. 3.26. 2nd derivative of the logarithmic model with a refitted x axis.

With the exception of dry season mid canopy dipteran abundance, all the other models show a contracted, almost random effect far within the boundary of the forest with seemingly no effect right at the edge of the forest where one would expect to see it. It is therefore entirely possible that these models (with the exception the mid canopy Diptera) have failed to show a true relationship.

Taking this into consideration only the extent of the edge effect penetration for mid canopy dry season Diptera was calculated, this is done by solving the equation for *x* at the maxima and minima of the curve. In this case the effect is at its greatest between 53 m and 114 m within the forest boundary.

3.3.3.3.3 Unimodal model

Finally, (following Ewers and Didham (2006)) we arrive at the last model fit. According to Ewers and Didham, the previous logarithmic model may work better with multiple edges and a unimodal model (only a slight modification of the logarithmic model) may fit edge data more efficiently.

As with the previous analysis, the model can become unstable very easily especially if the minimum and maximum constants fall outside of the data range. Therefore during analysis minimum temperature, maximum humidity and distance to nearest vegetation were discounted as the models produced fell into this category. However results from the other parameters were more encouraging. Table 3.5 (below) shows the results of the constants, model fit and residuals.

Table 3.5 Unimodal model analysis

Dependent	season	transect	B_0	B_1	B_2	B_3	B_4	R^2	Stable SE	mode assum
Log10	Dry	Ground	0.86	1.79	-5.74	0.035	-0.007	0.29	Yes	Yes
Diptera		Mid	-180.01	1.40	-815.1	0.007	-0.270	0.46	No	No
Abundance		High	-	-	-	-	-	-	-	-
	Wet	Ground	1.03	1.29	-8.47	4.149	-0.004	0.17	Yes	No
		Mid	0.88	1.32	-6.07	6.467	-0.031	0.18	Yes	Yes
		High	0.85	1.32	-7.69	5.877	-0.028	0.22	No	Yes
Maximum	Dry	Ground	43.22	32.3	-35.14	0.054	-0.011	0.17	No	Yes
Temp ºC		Mid	-	-	-	-	-	-	-	-
		High	38.95	34.2	-17.12	0.535	-0.110	0.35	Yes	Yes
	Wet	Ground	32.56	27.1	-13.91	-0.55	-0.005	0.60	Yes	Yes
		Mid	29.87	32.8	-9.42	1.63	-0.014	0.17	Yes	No
		High	28.73	34.2	-6.91	0.13	-0.016	0.19	Yes	Yes
Minimum	Dry	Ground	-	-	-	-	-	-	-	-
Humidity		Mid	67.35	18.4	-75.22	0.11	-0.003	0.65	Yes	Yes
		High	49.16	19.8	-881.7	0.005	0.062	0.61	No	Yes
	Wet	Ground	85.81	67.1	-11.90	0.401	-0.005	0.34	Yes	Yes
		Mid	68.93	23.1	-83.09	-0.072	-0.003	0.20	Yes[†]	Yes
		High	-	-	-	-	-	-	-	-

- Unstable/non fitting model

[†] Standard error borderline

B_x Constants from the equation

R^2 Unimodal fit

SE Standard error

As before, models were only considered stable if all residual assumptions were met, iteration limits were not exceeded and standard errors were reasonable. Eight of the

subsequent analysis showed signs of stability using this analysis, they were; dry season ground canopy and wet season mid canopy dipteran abundance, dry season high canopy and wet season ground and high canopy maximum temperature and dry season mid canopy and wet season ground and mid canopy minimum humidity.

Table 3.6. Magnitude of effects taken from the unimodal regression equation.

Dependent	Season	Transect (canopy Hight)	Min Value	Max Value	Magnitude	Extent
Log 10 Diptera Abundance	Dry	Ground	0.861	1.101	0.240	*30 to -179
	Wet	Mid	0.884	0.884	1.18E-6	-7 to -24
Maximum Temperature ºC	Dry	High	34.249	34.251	0.002	0 to -9
	Wet	Ground	27.064	27.064	1.13E-8	†
	Wet	High	28.734	30.100	1.365	6 to -69
Minimum Humidity %RH	Dry	Mid	18.438	53.055	34.617	-76 to -258
	Wet	Ground	67.068	85.814	18.746	-9 to -192
	Wet	Mid	23.084	45.801	22.717	-70 to -264

† both points lay outside of range of data

† effect went beyond 30 m into the savannah

To calculate the extent of the effect within the unimodal analysis one must take the two maxima or minima point along the 2nd derivative curve. This indicates the two *x* values between which the effect has its greatest influence (Ewers and Didham, 2006). In fig.2.27, below, we can see that the effect in maximum temperature within the high canopy during wet season has is at its greatest between 6 m into the savannah matrix and 69 m into the forest edge. The results are displayed in table 3.6, above.

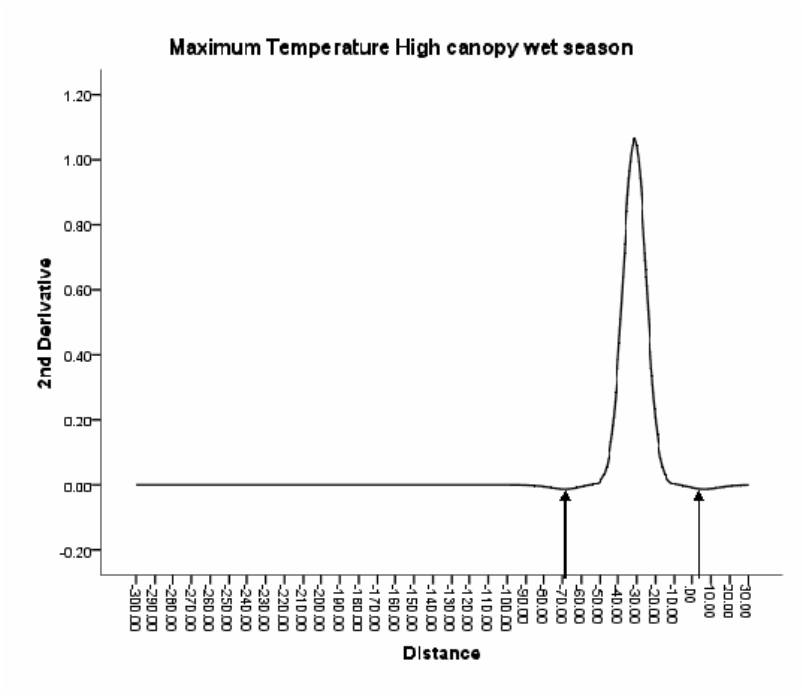


Fig. 3.27. Example of 2nd derivative unimodal curve and the calculation of edge effect extent.

3.3.3.3.4 Assessment of model fit

Table 3.7. Akaike weight calculations for fitted models, see section 3.3.3.2 for definitions of components

Dependent	Season	Transect	Model	K	RSS	AIC_c	Δ_i	w_i
Diptera Abundance	Dry	Ground canopy	Linear	3	4.142	-77.518	56.387	0.00
			Power	-	-	-	-	-
			Logarithmic	5	7.179	-122.67	11.306	0.003
			Unimodal	6	5.75	-133.91	0.00	0.997
		Mid Canopy	Linear	3	3.493	-97.819	0.00	0.690
			Power	4	3.445	-95.950	1.868	0.271
			Logarithmic	5	3.599	-91.528	6.291	0.030
			Unimodal	6	3.578	-89.040	8.778	0.009
		High Canopy	Linear	3	4.366	-81.935	N/A	N/A
			Power	-	-	-	-	-
			Logarithmic	-	-	-	-	-
			Unimodal	-	-	-	-	-
	Wet	Ground canopy	Linear	3	3.064	-106.97	35.262	0.000
			Power	4	3.056	-104.64	37.587	0.000
			Logarithmic	5	3.864	-142.23	0.00	0.698
			Unimodal	6	3.808	-140.55	1.671	0.302
		Mid Canopy	Linear	3	6.29	-84.954	74.822	0.000
			Power	4	5.77	-86.519	73.257	0.000
			Logarithmic	5	1.111	-159.77	0.00	1
			Unimodal	6	5.327	-85.015	74.760	0.000

		High Canopy	Linear	3	3.867	-100.40	0.100	0.354
			Power	4	3.702	-99.89	0.607	0.274
			Logarithmic	-	-	-	-	-
			Unimodal	6	3.241	-100.50	0.00	0.372
Minimum Humidity	Dry	Ground canopy	Linear	3	3982.6	113.379	N/A	N/A
			Power	-	-	-	-	-
			Logarithmic	-	-	-	-	-
			Unimodal	-	-	-	-	-
		Mid Canopy	Linear	3	2919.20	111.04	0.00	0.693
			Power	4	2898.97	113.98	2.342	0.160
			Logarithmic	5	2494.31	114.32	3.285	0.134
			Unimodal	6	2554.98	118.83	7.790	0.014
		High Canopy	Linear	3	2704.65	109.43	0.00	0.764
			Power	4	2694.80	112.45	3.012	0.169
			Logarithmic	-	-	-	-	-
			Unimodal	6	2411.26	114.31	4.871	0.067
	Wet	Ground canopy	Linear	3	2419.72	110.74	0.00	0.742
			Power	4	2485.82	114.35	3.012	0.122
			Logarithmic	-	-	-	-	-
			Unimodal	6	1770.64	114.14	4.871	0.136
		Mid Canopy	Linear	3	2422.42	110.77	0.00	0.699
			Power	4	2370.85	113.31	2.546	0.196
			Logarithmic	5	2184.59	114.91	4.143	0.088
			Unimodal	6	2134.09	118.25	7.479	0.017

		High Canopy	Linear Power Logarithmic Unimodal	3 - - -	2105.68 - - -	107.68 - - -	N/A - - -	N/A - - -
Maximum Humidity	Dry	Ground canopy	Linear Power Logarithmic Unimodal	3 4 - -	2644.23 2226.43 - -	105.19 104.91 - -	0.273 0.00 - -	0.466 0.534 - -
		Mid Canopy	Linear Power Logarithmic Unimodal	3 4 - -	2062.04 1700.50 - -	103.737 102.777 - -	0.960 0.00 - -	0.382 0.618 - -
		High Canopy	Linear Power Logarithmic Unimodal	3 4 - -	2348.98 2069.31 - -	102.82 103.45 - -	0.00 0.631 - -	0.578 0.422 - -
	Wet	High Canopy	Linear Power Logarithmic Unimodal	3 4 - -	0.909 0.806 - -	-62.77 -62.40 - -	0.00 0.374 - -	0.547 0.453 - -
Minimum Temperature	Dry	Ground canopy	Linear Power Logarithmic Unimodal	3 4 - -	68.029 57.632 - -	31.984 31.830 - -	0.154 0.00 - -	0.481 0.519 - -

		Mid Canopy	Linear Power Logarithmic Unimodal	3 4 5 -	74.147 73.341 61.395 -	33.904 36.737 36.529 -	0.00 2.859 2.625 -	0.663 0.158 0.178 -
		High Canopy	Linear Power Logarithmic Unimodal	3 4 - -	72.480 71.349 - -	33.252 36.104 - -	0.00 2.852 - -	0.806 0.194 - -
	Wet	Ground canopy	Linear Power Logarithmic Unimodal	3 4 - -	15.700 15.364 - -	-0.089 2.455 - -	0.00 2.544 - -	0.781 0.219 - -
		Mid Canopy	Linear Power Logarithmic Unimodal	3 4 - -	18.347 16.707 - -	3.339 4.298 - -	0.00 0.960 - -	0.618 0.382 - -
		High Canopy	Linear Power Logarithmic Unimodal	3 4 - -	22.273 21.979 - -	7.605 10.332 - -	0.00 2.727 - -	0.796 0.204 - -
Maximum Temperature	Dry	Ground canopy	Linear Power Logarithmic Unimodal	3 - - 6	223.826 - - 211.725	55.803 - - 65.653	0.00 - - 9.850	0.993 - - 0.007

		Mid Canopy	Linear Power Logarithmic Unimodal	3 4 - -	243.414 258.753 - -	58.867 63.238 - -	0.00 4.372 - -	0.899 0.101 - -
		High Canopy	Linear Power Logarithmic Unimodal	3 4 - 6	189.779 203.019 - 135.206	52.503 57.018 - 56.683	0.00 4.515 - 4.180	0.814 0.085 - 0.101
	Wet	Ground canopy	Linear Power Logarithmic Unimodal	3 4 - 6	160.299 150.024 - 69.892	51.025 52.588 - 43.030	7.995 9.558 - 0.00	0.018 0.008 - 0.974
		Mid Canopy	Linear Power Logarithmic Unimodal	3 - - 6	239.102 - - 211.348	59.822 - - 67.347	0.00 - - 7.552	0.978 - - 0.022
		High Canopy	Linear Power Logarithmic Unimodal	3 - - 6	269.051 - - 273.784	62.418 - - 73.069	0.00 - - 6.384	0.961 - - 0.039
Log Distance to nearest vegetation	Ground canopy		Linear Power Logarithmic Unimodal	3 - 5 -	0.247 - 0.334 -	-184.66 - -168.03 -	0.00 - 16.636 -	1.000 - 0.000 -

	Mid Canopy	Linear	3	1.458	-41.180	0.602	0.425
		Power	4	1.190	-41.782	0.00	0.575
		Logarithmic	-	-	-	-	-
		Unimodal	-	-	-	-	-
	High Canopy	Linear	3	0.999	-41.180	0.00	0.988
		Power	4	1.190	-38.278	8.828	0.012
		Logarithmic	-	-	-	-	-
		Unimodal	-	-	-	-	-

From table 3.7, above, the results show that the linear and power models worked best with the environmental factors where as the dipteran samples containing the savannah matrix data performed better with the logarithmic and unimodal models.

When interpreting these results one must remember that w_i can be interpreted as the probability that *i* is the best model given the data and the set of models, each number is therefore only relevant to other weights within a given dependent model set. For example if we look at the results of maximum humidity along the mid canopy transect in the dry season, we can see that w_i is 0.547 and 0.453 for linear and power models respectively. Therefore the linear model is only (0.547/0.453) = 1.2 times more likely than the power model. In general the confidence set of candidate models include models that are within 10% of the highest. So in this respect we can actually accept models that have a w_i of more than (0.547*0.1) = 0.056, as it would mean that the candidate model with the lower w_i is within 10 times as likely as the higher performing model. This means that in many cases we can accept more than one model as a fit, and therefore use the mathematical properties that are inherent in the non linear regression lines.

3.3.3.4 Edge Effect Conclusions

This section set out to determine whether discernable edge effects could be found within the data. Using the models suggested by Ewers & Didham (2006) edge effects have to some degree been confirmed in the dipteran populations, environmental parameters and structural attributes even at this broad scale. In general, the higher models (logarithmic and unimodal) did not perform well without the added data from the savannah matrix, however with those data included the models did provide information on the presence of the effect, its midpoint, magnitude and extent. Therefore this confirms Ewers and Didham's theory that these higher level models are suitable when analysing data of this type.

Using a tool kit of models such as this is not really about trying to find the exact nature of the relationship, but more about finding which type of relationship fits with that particular data set, and then using the mathematical attributes of each regression line to discern further information when possible. For example it is not whether or not the dipteran abundance forms a linear or unimodal relationship with distance from the edge that is important here, it's more a question of detecting if there is an effect and how far that effect stretches into the forest, and how changes in habitat (natural or anthropogenic) impact on that effect. Being able to use either the logarithmic or unimodal models allows us to do this, and even the power model provides data on the midpoint of the effect. The mid point can still be used as a marker, for example, if burning of the savannah moves the mid point of the effect 100 m further into the interior of the forest, we then know that burning adjacent savannah increases the extent of the edge effect.

It must also be pointed out that only distance from the edge has been used as an independent factor this analysis, and that environmental parameters could be used as

independent factors as well. For example, temperature, humidity and rainfall are all factors that have been reported (see Costa et al. (2010) for example) to affect Diptera populations. In the analysis reported in this chapter, environment data were split over seasonal divides and treated as a spatial artefact of its position from the edge of the forest. However environmental data could be seen as a gradient itself and its relationship with the abundance of Diptera investigated in the same way as above. Using these environmental parameters as dependents may also go some way to understanding the possible effects of future climate change. For example, correlation analysis of transformed Diptera abundance against minimum/maximum humidity and rain fall (mm) show highly significant relationships within this data set, $r = 0.353, 0.497, 0.359$ respectively (all P values <0.001), minimum and maximum temperature did not show significant relationships, $r = 0.099$ and -0.129 respectively.

The next stage of this analysis will concentrate on specific taxanomic groups and families of Diptera from the samples collected to see if these models can show specific effect of edge at the suborder and family level. It will also be interesting to investigate if these models (or related models) could help to determine the effect of height within the canopy on dipteran families, using height as the independent factor rather than distance from the edge of the forest. Later chapters will also investigate the effects of treatment and seasonality in more detail than shown here.

Chapter 4: Height effects and seasonality of dipteran communities in a Nigerian tropical forest.

4.1 Introduction

This chapter will primarily be investigating what role height plays in affecting the abundance and community structure of Diptera in the Kwano Forest. In chapter 3 we saw that without taking seasonality into account there is no overall difference in total Diptera abundance over the three height classes (ground, mid and high canopy); however, when taking seasonality into account there seems to be a shift in abundance between the ground canopy and the mid and high canopy (see fig 3.16, and 3.20 for details). The analysis showed that during the dry season the ground canopy had a significantly higher abundance of Diptera than both the mid and high canopy. However once the rains had started the mid and high canopy significantly increased and the ground canopy abundance decreased to a point where the mid and high canopy had a significantly higher abundance than the ground.

Therefore this chapter will consider individual taxanomic groups and families of Diptera over the wet and dry season and look for the underlying factors that are driving their community structure through the vertical gradient. The literature points to Diptera abundance increasing during the wet season (Breidenbaugh et al., 2009, de Araujo and dos Santos, 2009, dos Santos et al., 2010), which is certainly what the data in this thesis indicates (see Chapter 3), but the underlying mechanisms are not always as clear cut. Environmental conditions are often cited as being the major driving force for changes in Diptera abundances and community structure with temperature and humidity being frequently cited parameters (see Costa et al. (2010), Costa-Lima et al. (2010), and Vargas et al. (2010) for examples). The Kwano study site is directly affected by the West African

Monsoon, where increasing seasonal solar radiation inundates the region with a continuous rainy season from mid March until mid October. This increased rain significantly increases relative humidity and significantly reduces maximum daily temperatures (Miller et al., 2009) Therefore changes in temperature and humidity are really only a secondary effect of the presence or absence of rain/cloud cover.

There are very few studies which have investigated the seasonal effects on vertical stratification of Diptera. This study will attempt to combine these two effects and look at the changes in dipteran communities across the seasons and through the vertical gradient.

4.2 Methodology

Data collection and site selection are as in the previous chapters (see Chapter 2); however here the distance and treatment data are pooled so that the effects of height and season can be investigated across the entire forest habitat. Only data from the forest has been used here, excluding the savannah data as the community of Diptera is different to that found in the forest, and as savannah data were only collected from the ground, it would unbalance the samples.

Previously seasonal analysis in this thesis has used the standard, but somewhat arbitrary categories of wet and dry season; however as we saw in the regression analysis in Chapter 3, there was some overlap in seasonal data towards the end of the second dry season. Therefore in this analysis the seasonal categories of 'rain' and 'no rain' are investigated to see if they provide more accurate information on the effect of seasonality and rainfall. The term 'rain' simply refers to days when rain was recorded at the study site, and 'no rain' to days when rain was not recorded at the study site. This grouping should provide

information not only on the seasonal abundance of Diptera but also on the behaviour of Diptera during periods of rain, because there were days in the wet season where there was no rain and there are several days in the dry season where there was rain.

A mixture of parametric and non parametric tests was used to explore these data. Normality was tested using a one-sample Kolmogorov-Smirnov test, and where $p > 0.05$ normality was assumed. Where the normality of the data allowed parametric tests were used, these consisted of one and two way ANOVA's with Tukey's post hoc tests. These data consisted of the environmental parameters (between season differences) and total dipteran abundance. Where the data were not normally distributed a series of Kruskal-Wallis tests were used with Mann-Whitney post hoc analysis where necessary, therefore environmental parameters (differences between heights), suborder and family level data were tested following this method. As all sample sizes within the Mann Whitney U tests were above 41, therefore z-approximation scores are reported rather than the U statistic (Green and Salkind, 2008), these are simply referred to '*z*' in the results and all are negative. Where there was a danger of type one errors occurring with multiple Mann-Whitney tests a Bonferroni correction was employed. The Bonferroni correction was calculated using the formula below.

$$\alpha_{new} = \frac{\alpha_{old}}{C}$$

Where α_{old} = the original significance level, α_{new} = the corrected significance level and C = the number of comparisons to be made. As there were never more than three comparisons to be made within each of the calculations $\alpha_{new} = 0.016$, therefore only *p* values < 0.016 were accepted as significant. As there are many significant and non significant results analysed a results summary table is placed at the end of each section.

4.3 Results

4.3.1 Environmental Parameters Analysis

Chapter 3 showed that minimum humidity and maximum temperature were important in understanding total dipteran abundance. Therefore in this chapter their role in the vertical stratification and seasonal turnover will be investigated further. Both parameters were normally distributed without the need for a transformation. Therefore both parametric and non parametric analyse were used to look for specific differences in height and seasonal effects.

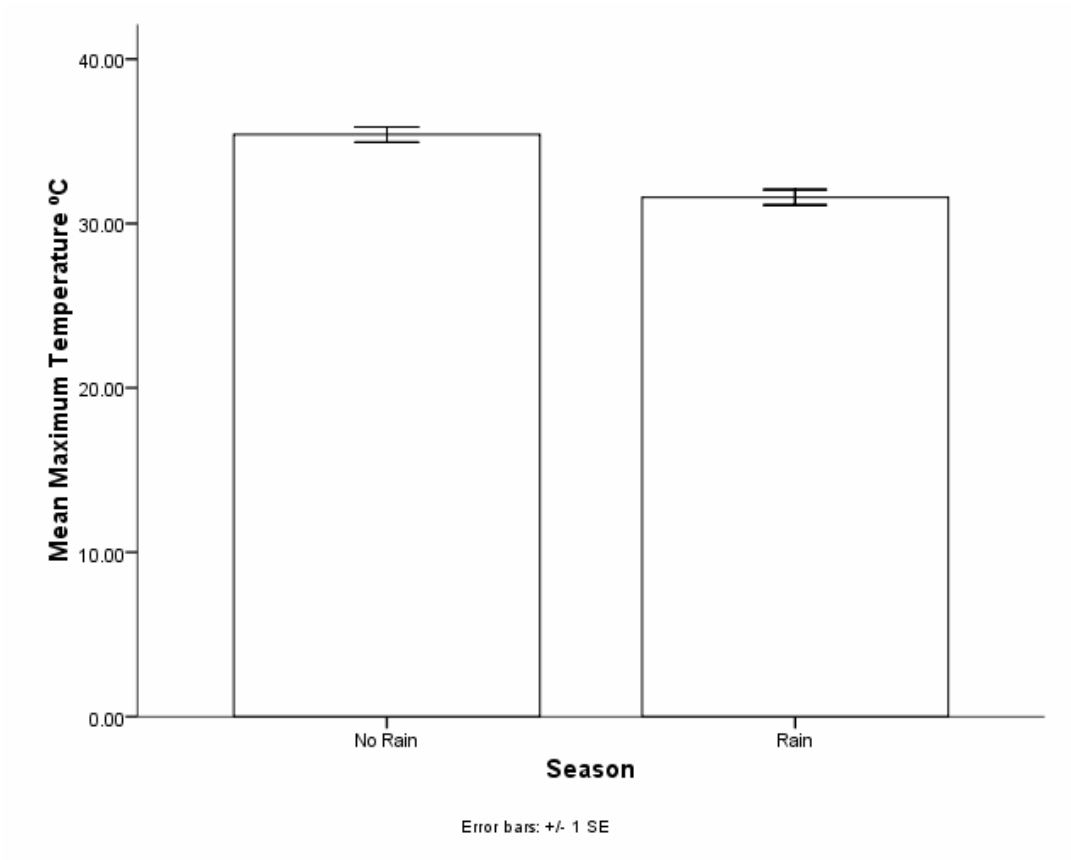
Seasonal variation in maximum temperature and minimum humidity were assessed. During the dry season mean maximum temperature was 35.5 ºC (*SD* = 3.06, *N* = 44) and mean minimum humidity was 26.7 %RH (*SD* = 19.0, *N* = 44). During periods of rain the mean maximum temperature dropped to 31.6 ºC (*SD* = 4.28, *N* = 83) and mean minimum humidity increased to 63.95 %RH (*SD* = 17.15, *N* = 83). This represents an 11 % decrease in maximum temperature and 240 % increase in minimum humidity between periods of no rain and rain. Maximum temperature decreases from 34.2– 29.9, 35.5 – 32.3 and 36.3 – 32.7 ºC, and minimum humidity increases from 34.2 – 71.1, 25.1 – 60.9 and 24.9 – 59.4 %RH at the ground, mid and high canopy respectively from periods of no rain to rain.

Initially a paired t-test was used to compare the environmental factors between periods of rain and no rain with sample locations grouped according to seasonal category. The minimum humidity and maximum temperature data for both seasons were transformed using a natural log transformation because ‘no rain’ data for minimum humidity were not normally distributed. The results showed that maximum temperature, was significantly

higher during periods of no rain, t = -5.707, df = 43, $p < 0.001$, r = 0.62, and that minimum humidity was significantly higher during periods of rain, t = -10.765, df = 43, $p < 0.001$, r = 0.85.

A one-way ANOVA was conducted on each of the seasonal categories to look for differences between the tree height classes. Data were split in SPSS 17 between periods of rain and no rain in order to analyse the data separately. The results of the one-way ANOVA showed that during periods of no rain there was no significant difference in either minimum humidity, F (2, 43) = 0.413, *ns*, or maximum temperature, F (2, 43) = 1.71, *ns*, between height classes. However during period of rain both minimum humidity, F (2, 82) = 4.193, $p < 0.05$, and maximum temperature, F (2, 82) = 3.92, $p < 0.05$, showed significant differences within each of the height categories (see fig 4.1 below). Tukey post hoc analysis found that the ground canopy had a significantly higher minimum humidity than the high canopy, $p < 0.05$, but that there was no significant difference between ground and mid canopy and mid and high canopy. Maximum temperature was significantly higher in the high canopy than in the ground canopy, $p < 0.05$, but again there were no significant differences between the ground and mid canopy and the mid and high canopy.

Finally the within height difference between seasons were investigated in the form of a Mann-Whitney test, which showed that both environmental parameters differed at all height classes between periods of rain and no rain, with maximum temperature higher during periods of no rain at the ground canopy, z = -3.28, p = 0.001, mid canopy, z = -2.63, $p < 0.01$, and high canopy, z = -2.90, $p < 0.005$. Whereas minimum humidity was higher during periods of rain at the ground canopy, z = -3.99, $p < 0.001$, mid canopy, z = -4.62, $p < 0.001$, and high canopy, z = -4.68, $p < 0.001$. Figure 4.2 shows the results.



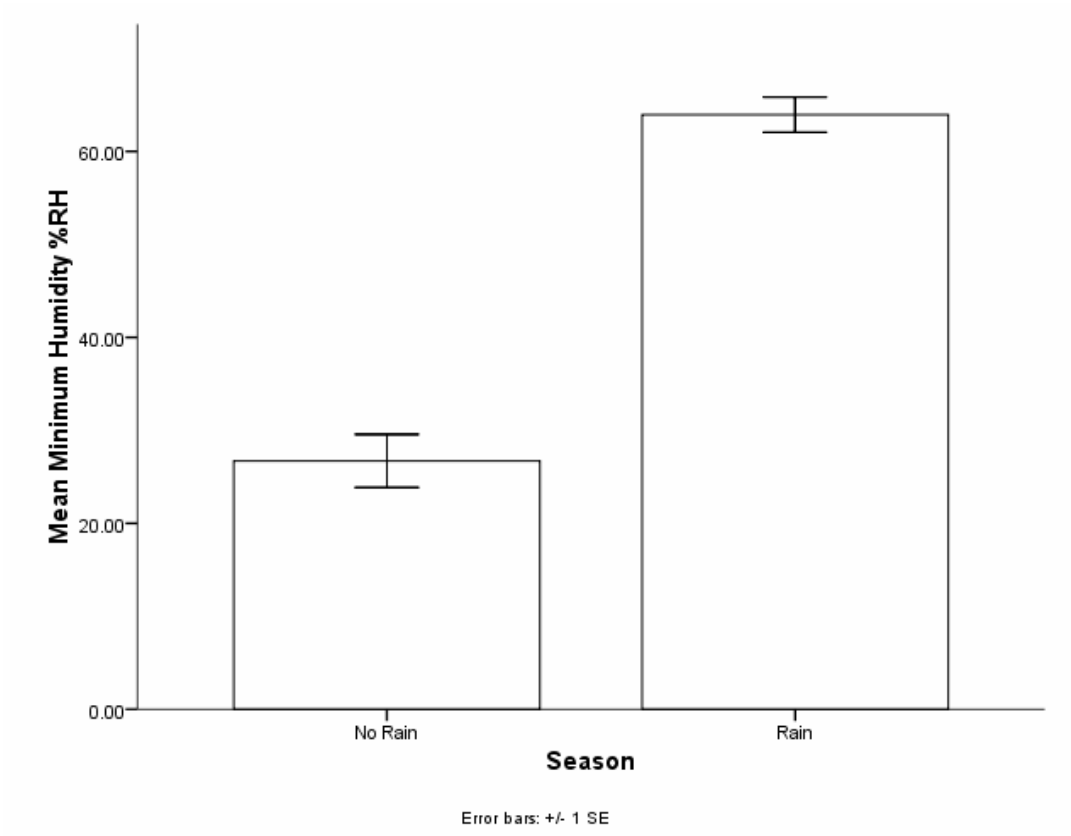


Fig 4.1. Differences in maximum temperature (top) and minimum humidity (bottom) during periods of rain and no rain, Kwano forest.

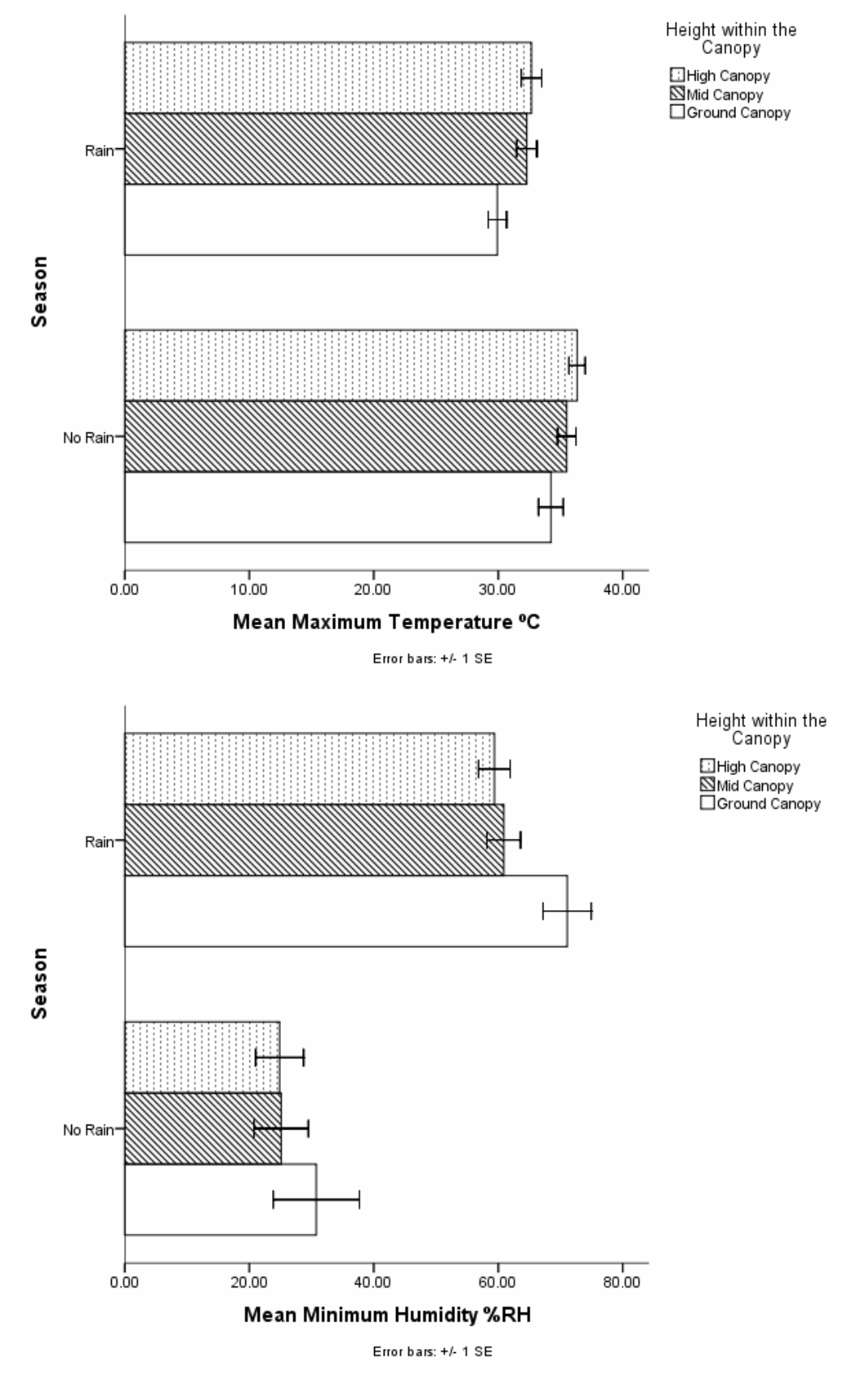


Fig 4.2. Differences in maximum temperature (top) and minimum humidity (bottom) within height classes across periods of rain and no rain, Kwaon forest.

Finally to discover if there is significant interaction between rain and height to the significant differences seen, a 2-way ANOVA was conducted on these two environmental parameters. Neither the maximum temperature, $F = 0.198$, $df = 2$, *ns*, or minimum humidity, $F = 0.281$, $df = 2$, *ns*, showed a significant interaction.

4.3.2 Total Diptera Abundance Analysis

A total of 4497 Diptera were sampled over the four seasons of field collection. In order to understand the complexities of the various Diptera life histories and physiology the order was divided initially into four sub categories. The first incorporates the entire suborder of the Nematocera; however as the suborder of Brachycera is a diverse group this was further subdivided into three categories, namely the Calyptrates, Acalyptrates and Other Brachycera (referred to as simply 'Brachycera' throughout the rest of the thesis). The later three subdivisions were chosen as they are simple to identify from each other and that each of these groups represent a particular combination of life history and ecology. The total sample set comprised of 81.9 % Nematocera, 7.7 % Brachycera, 5.6 % Acalyptrate and 4.7 % Calyptrate. During periods of no rain, mean Diptera abundance was 19.12 ($N = 33$, $sd = 14.90$) in the ground canopy, 9.77 ($N = 40$, $sd = 9.26$) in the mid canopy and 11.59 ($N = 37$, $sd = 14.12$) in the high canopy per trap day. Mean Diptera abundance during periods of rain were 17.56 ($N = 48$, $sd = 26.11$), 24.60 ($N = 48$, $sd = 23.91$) and 21.74 ($N = 47$, $sd = 17.19$) for ground mid and high canopy respectively per trap day.

To compare theses means statistically the data were first transformed using a natural log transformation as the data were not normally distributed. Introducing both elements (presents of rain and height within the canopy) into a two-way ANOVA shows that the presence of rain causes a significant differences in Diptera abundance, $F(1, 252) = 13.92$, $p < 0.001$, and that the interaction of rain and height also causes a significant difference in

Diptera abundance, F (2, 252) = 8.59, $p < 0.001$; however height alone does not, F (2, 252) = 0.81, $p > 0.05$ (although this is pooled rain and no rain data which has already shown no significant difference in previous analysis) (see Fig 4.3 below).

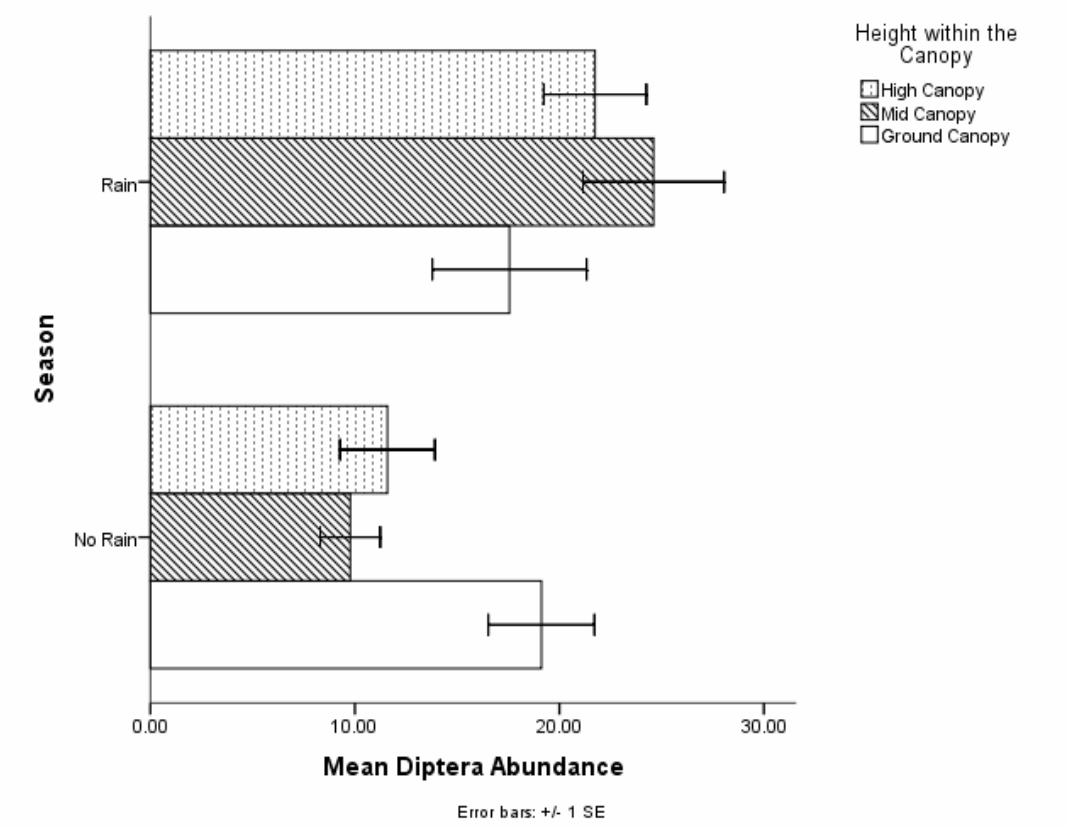
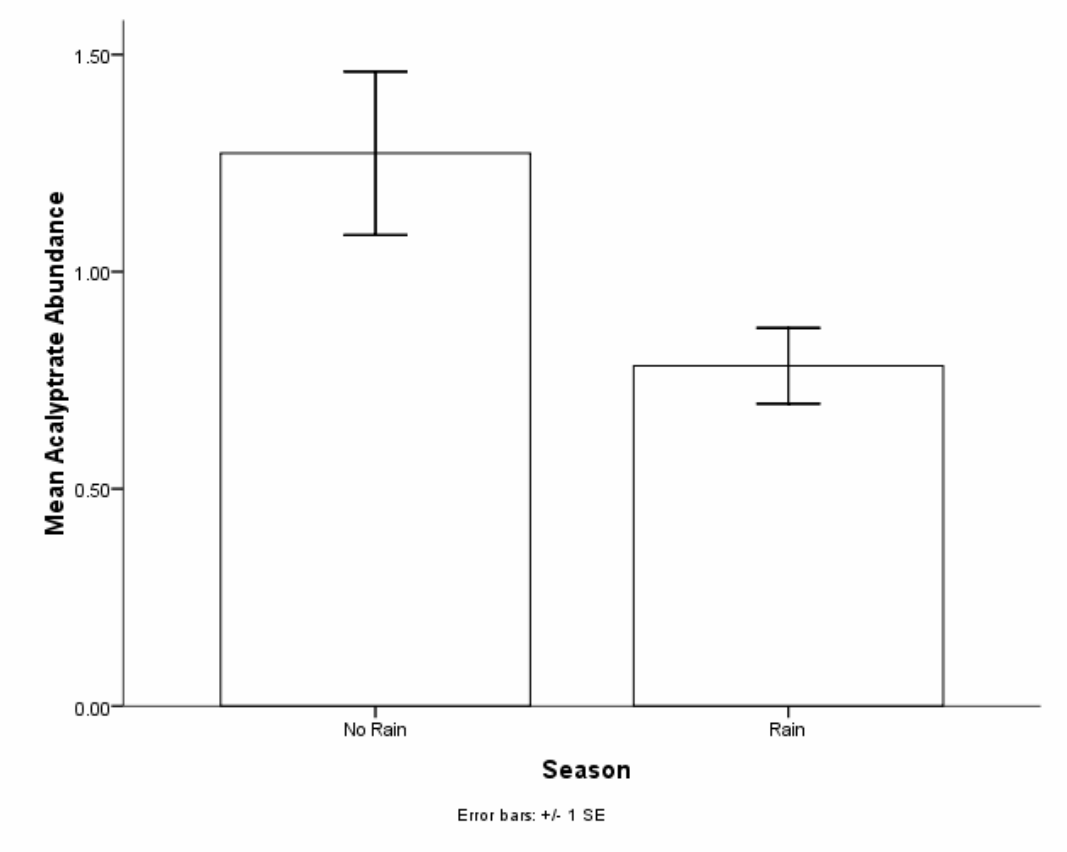


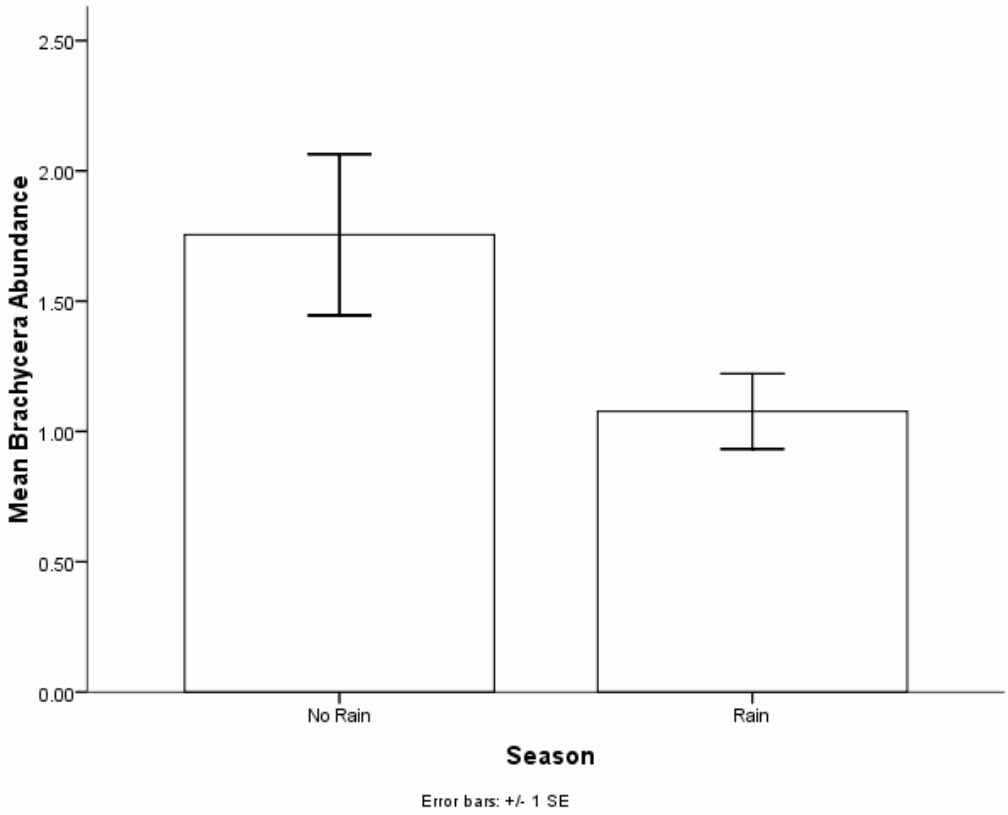
Fig 4.3 Mean dipteran abundance (per trap day) between periods of rain and no rain within different height classes, Kwano forest.

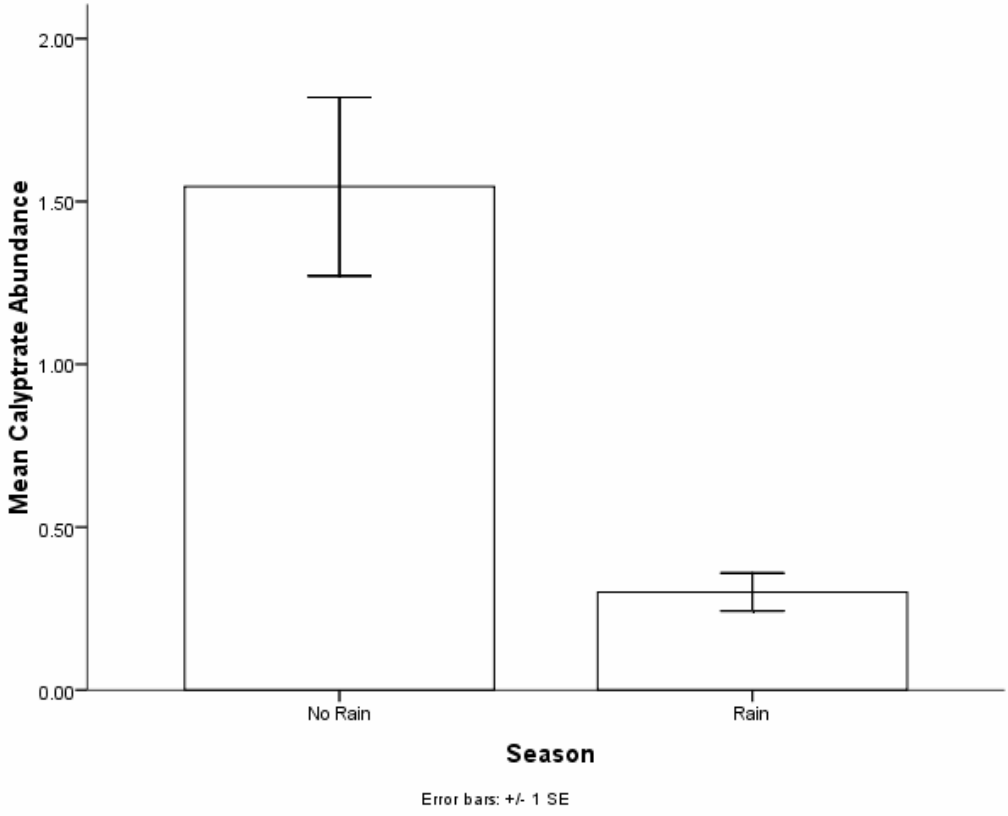
4.3.3 Sub Category Abundance Analysis

Non parametric analysis was used to investigate the effect of rain on individual sub categories of Diptera, namely; Nematocera, Brachycera, Acalyptrate and Calyptrate. Sub category abundances were not normally distributed and a natural log transformation only proved to normalise the distribution of Nematocera abundance therefore non parametric analysis was conducted all the untransformed data for consistency. The results showed that both the Nematocera, z = -5.52, $p < 0.001$, and Calyptrate, z = -4.35, $p < 0.001$, had

significantly different abundances in wet and dry periods, with Nematocera increasing in abundance during the rains and Calyptrate decreasing in abundance during the rains. The Acalyptrate and Brachycera categories showed no significant difference in abundance between periods of rain and no rain, z = -1.05, and z = -0.96 respectively. Figure 4.4, below, illustrates these relationships.




2.50
2.00
1.50
1.00
0.50
0.00
Mean Brachycera Abundance
No Rain
Rain
Season
Error bars: +/- 1 SE


2.00
1.50
1.00
0.50
0.00
Mean Calyptrate Abundance
No Rain
Rain
Season
Error bars: +/- 1 SE

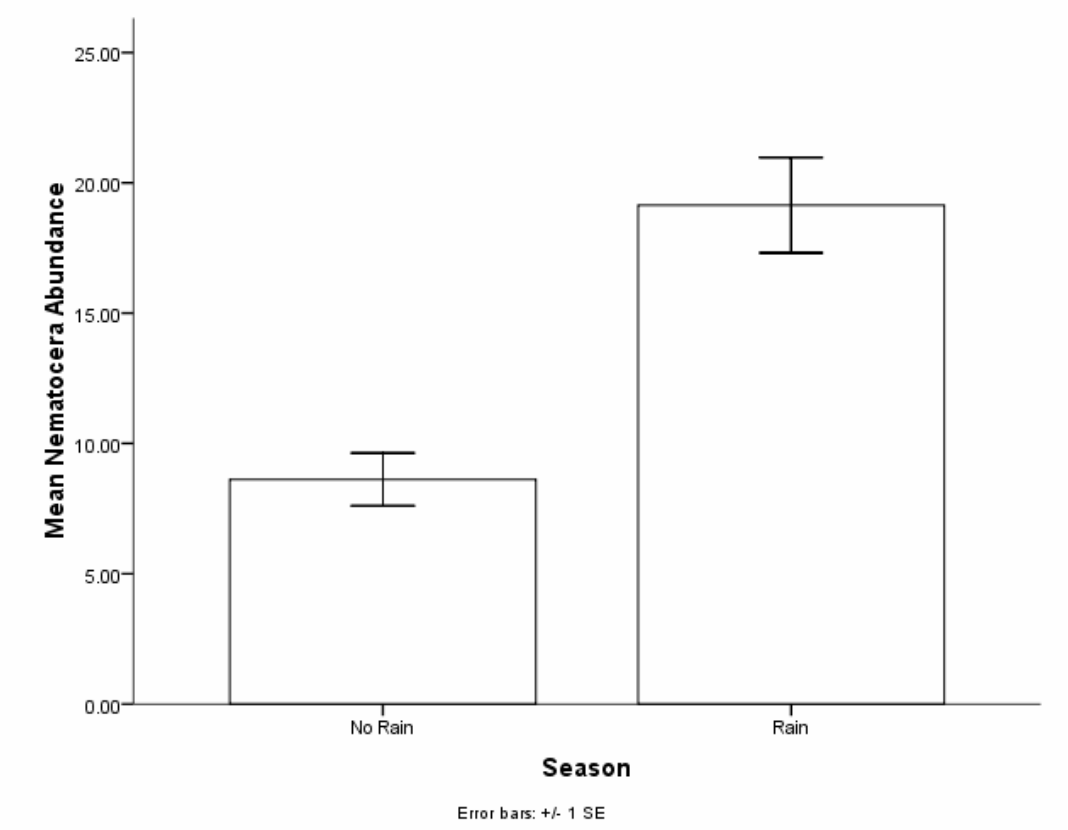


Fig 4.4 Effects of rainfall on dipteran suborder abundance (per trap day), Kwaon forest.

Data were then split by rain or no rain and a Kruskal-Wallis test was performed to look for significant differences between height classes within periods of rain or no rain. The significant and non significant interactions of this analysis are summarised in table 4.1 at the end of this section.

During periods of no rain Kruskal-Walllis tests showed the Acalyptrate (H = 7.80, df = 2, p < 0.05), Nematocera (H = 15.56, df = 2, p <0.001), and Brachycera (H = 10.10, df = 2, p < 0.05), all to have significant differences between height classes; however the Calyptrate did not. During periods of rain only the Acalyptrate and Brachycera both showed significant differences between height classes (H = 7.58, df = 2, p < 0.05, and H = 11.06, df = 2, p < 0.005 respectively) (see figure 4.5).

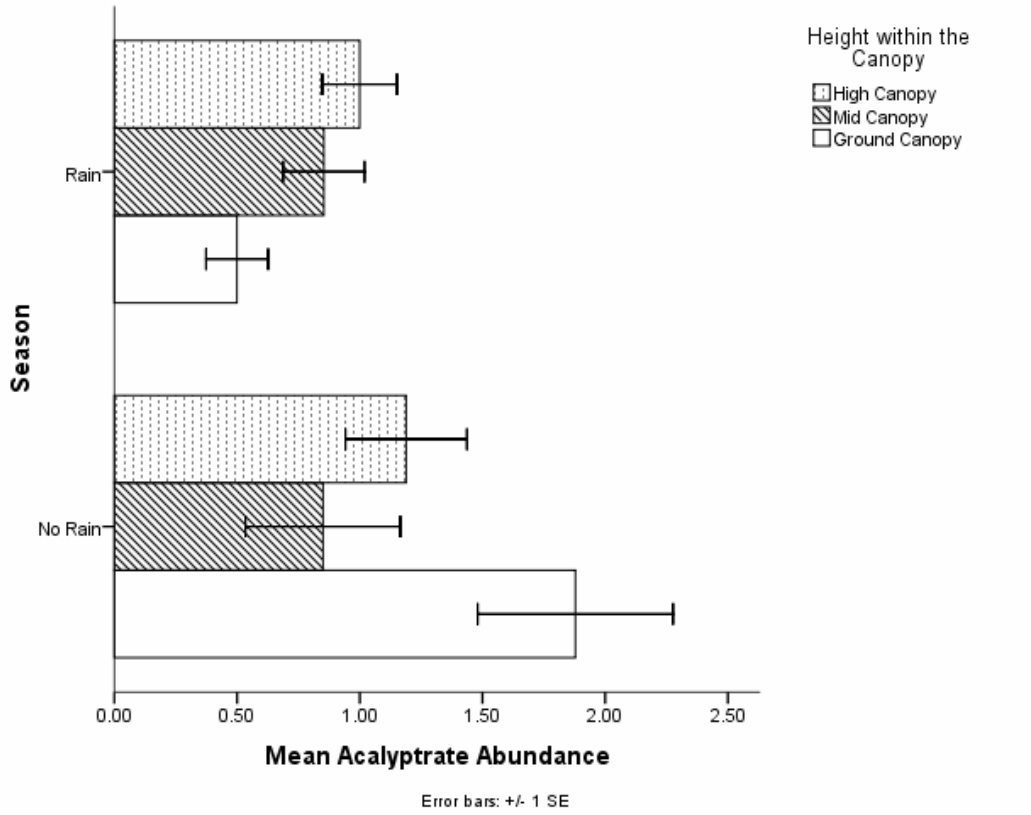
To test for specific differences between height classes a series of Mann-Whitney U tests were conducted, and to limit type one errors a Bonferroni corrected *p* was used. There were significantly higher abundances in the ground than the mid canopy samples during no rain periods in the Acalyptrate, $z = -2.54$, $p < 0.016$, Nematocera, $z = -2.94$, $p < 0.016$, and the Brachycera, $z = -3.09$, $p < 0.016$, but not in the Calyptrate. However during periods of rain all sub orders failed to meet the corrected *p* value.

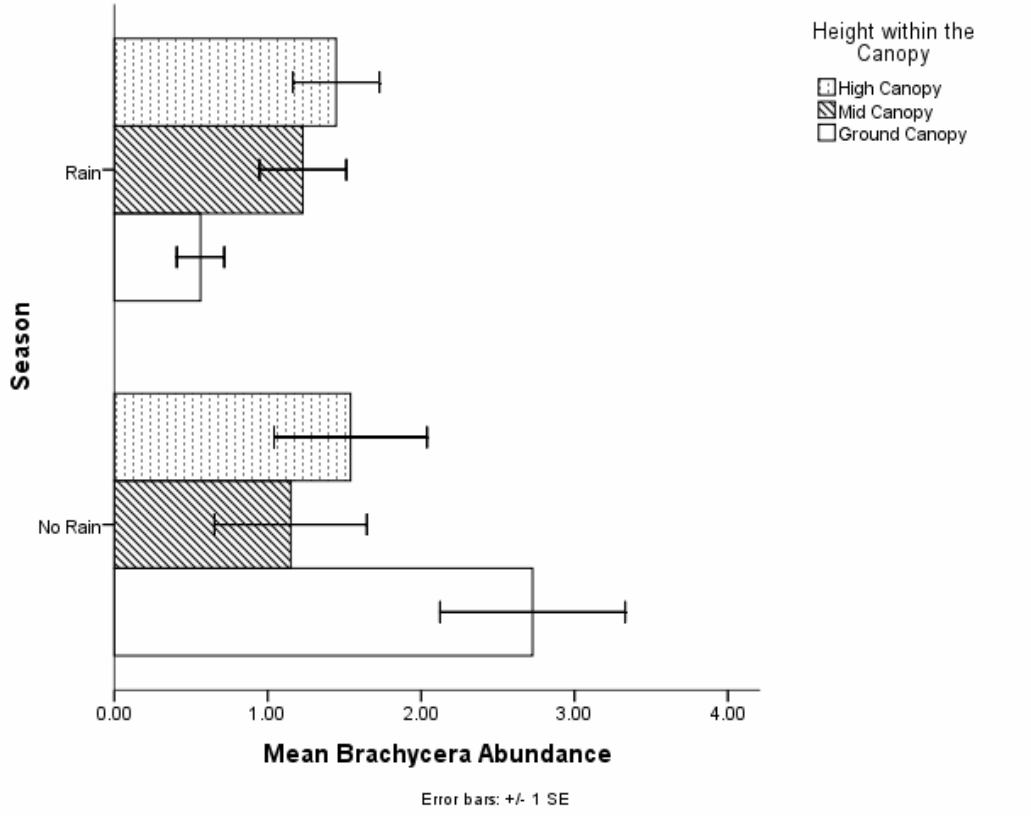
The results from the comparison of ground and high canopy showed that only the Nematocera showed a significantly higher abundance in periods of no rain, $z = -3.90$, $p < 0.001$. Acalyptrate, Brachycera, and Calyptrate all failed to meet the corrected *p* value. During periods of rain both Acalyptrate, $z = -2.66$, $p < 0.016$, and Brachycera, $z = -3.50$, $p < 0.001$, showed significantly higher abundances in the high canopy compared to the ground canopy. Both Nematocera and Calyptrate failed to meet the corrected *p* value.

There were no significant differences between mid and high canopy samples in either periods of rain or no rain in any of the sub order abundances, all failed to produce values below that of the corrected *p* value.

To test for the between-season effects of rain, each height was compared using a Mann-Whitney test. As only one comparison was needed per height (between rain and no rain) no Bonferroni correction was needed. Ground canopy samples showed significant differences in abundance of Acalyptrates, $z = -2.98$, $p < 0.005$, Brachycera, $z = -3.98$, $p < 0.005$ and Calyptrates, $z = -3.20$, $p < 0.001$, but not in the Nematocera. The mid canopy results showed that only Nematocera had a significant increase in abundance between periods of rain and no rain, $z = -4.208$, $p < 0.001$. All other groups showed no significant difference between periods of rain and no rain. In the high canopy Nemotocera, $z = -4.946$, $p < 0.001$, and Calyptrate, $z = -2.61$, $p < 0.01$, showed significantly different abundance

between the rain and no rain periods. Nematocera showed a significant increase during periods of rain and Calyptrates showed significant decreases during periods of rain. Neither Acalyptrate nor Brachycera abundances differed significantly between rain and no rain periods. Figure 4.5 below shows how the abundance of these sub orders of Diptera varies over height classes and periods of rain and no rain.


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
0.00
0.50
1.00
1.50
2.00
2.50
Mean Acalyptrate Abundance
Error bars: +/- 1 SE


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
0.00
1.00
2.00
3.00
4.00
Mean Brachycera Abundance
Error bars: +/- 1 SE

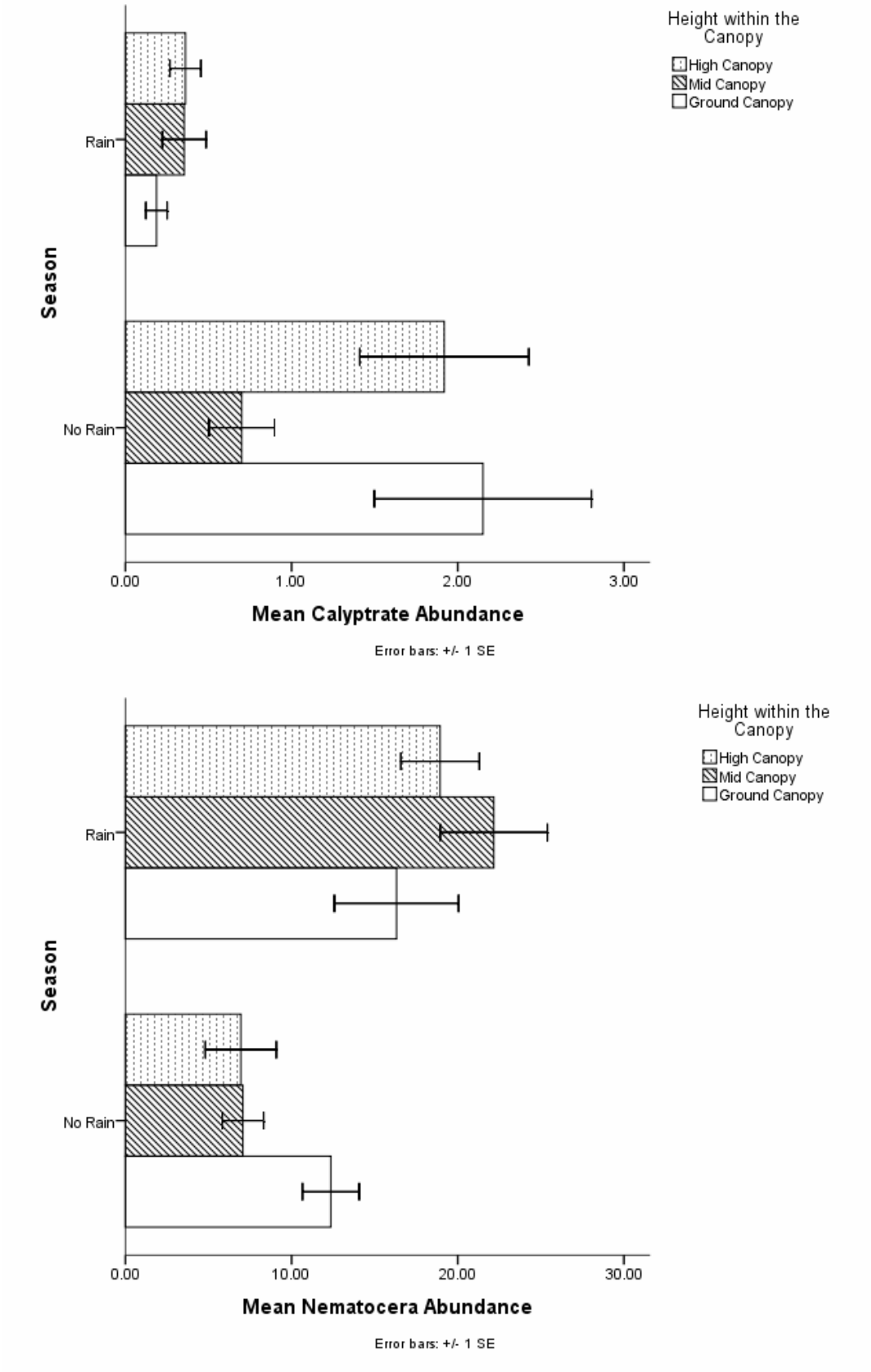


Fig 4.5 Sub order dipteran abundance (per trap day) at ground, mid and high canopy during periods of rain and no rain, Kwano forest.

Table 4.1 Summary of interactions of Diptera groups to height and season, match each column to a row to see if there is a significant difference (*) or non significant difference (*ns*) between factors, see fig 4.5, above, for magnitude and direction of effect.

Nematocera

Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*ns*	*		*	
Ground Wet			*ns*			*ns*		*ns*
Mid Dry			*			*	*ns*	
Mid Wet				*ns*	*			*ns*
High Dry			*		*ns*			*
High Wet				*ns*		*ns*	*	

Brachycera Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		ns						
No Rain	ns							
Ground Dry				*	*		*ns*	
Ground Wet			*			*ns*		*
Mid Dry			*			*ns*	*ns*	
Mid Wet				*ns*	*ns*			*ns*
High Dry			*ns*		*ns*			*ns*
High Wet				*		*ns*	*ns*	

Acalyptrate Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*ns*						
No Rain	*ns*							
Ground Dry				*	*		*ns*	
Ground Wet			*			*ns*		*
Mid Dry			*			*ns*	*ns*	
Mid Wet				*ns*	*ns*			*ns*
High Dry			*ns*		*ns*			*ns*
High Wet				*		*ns*	*ns*	

Calyptrate Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*	*ns*		*ns*	
Ground Wet			*			*ns*		*ns*
Mid Dry			*ns*			*ns*	*ns*	
Mid Wet				*ns*	*ns*			*ns*
High Dry			*ns*		*ns*			*
High Wet				*ns*		*ns*	*	

4.3.4 Analysis of the Nematocera suborder

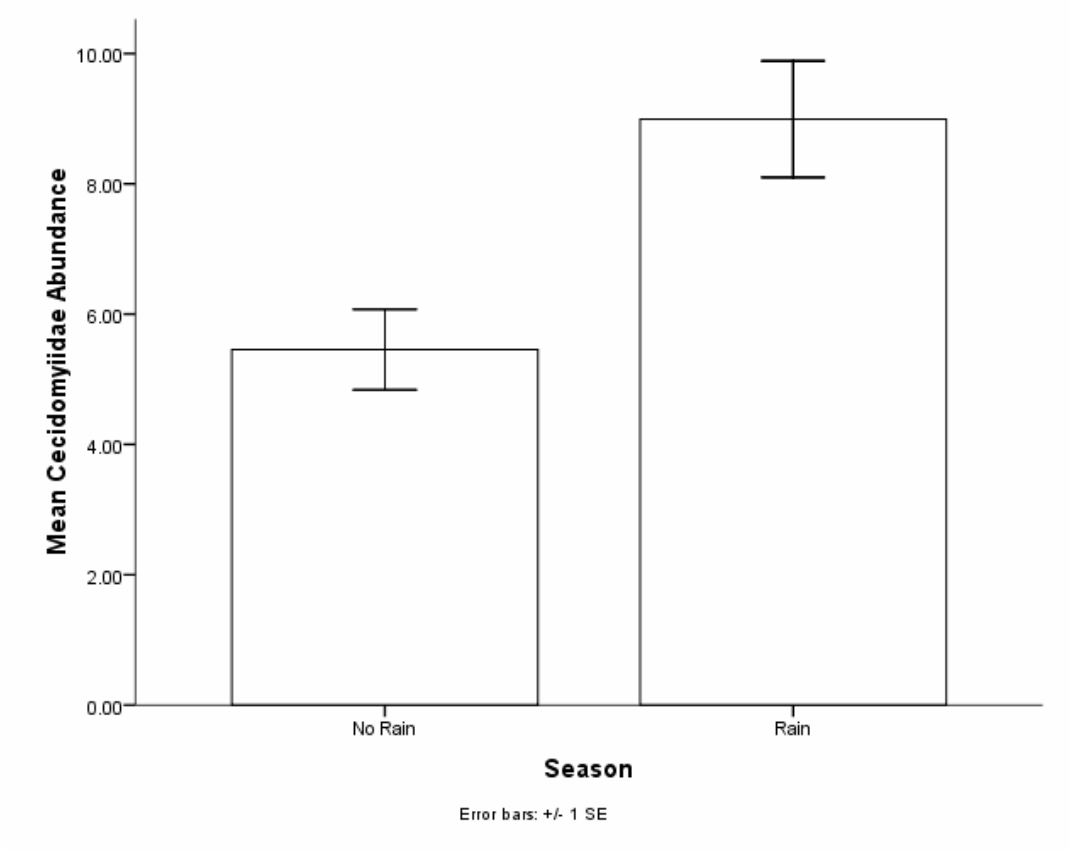
The nematoceran suborder represents the most abundant of all suborders in the samples collected, comprising of 3685 individuals and 81.9 % of total dipteran abundance across all samples. They are therefore an important component of the dipteran community in the Kwano forest. In the following section the nematoceran community structure and the way in which rainfall and height affects it will be analysed in more detail.

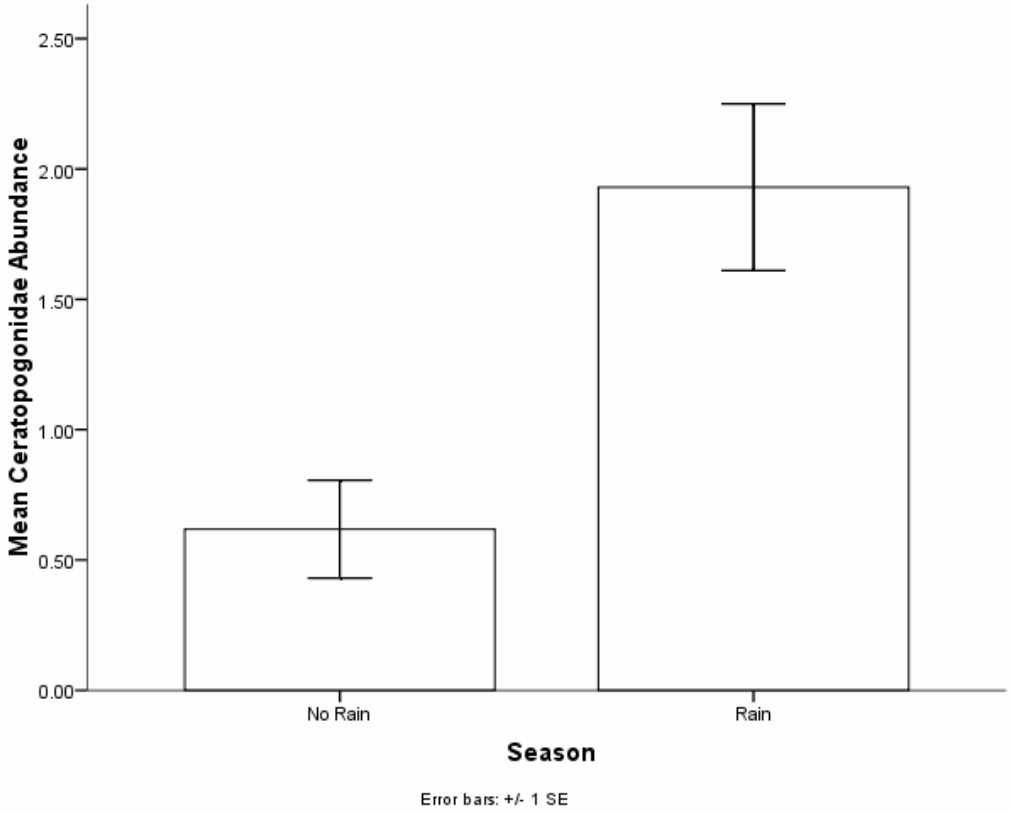
A total of 10 families and 1 subfamily of Nematocera were identified from the samples (% in parentheses represent % of Nematocera abundance); Tipulidae (1.7 %), Ceratopogonidae (9.3%), Culicidae (0.4%), Sciaridae (9.3 %), Simuliidae (0.7 %), Scatopsidae (0.8 %), Mycetophilidae (4.1 %), Psychodidae (2.1 %), Chironomidae (18.9 %), Cecidomyiidae (51.2 %) and Lestermiinea (1.0 %) (subfamily of the Cecidomyiidae). Only families that contributed more than 3 % of total Nematocera abundance are analysed here, therefore Tipulidae, Culicidae, Simuliidae, Scatopsidae, Psychodidae and Lestermiinea are discounted from this analysis.

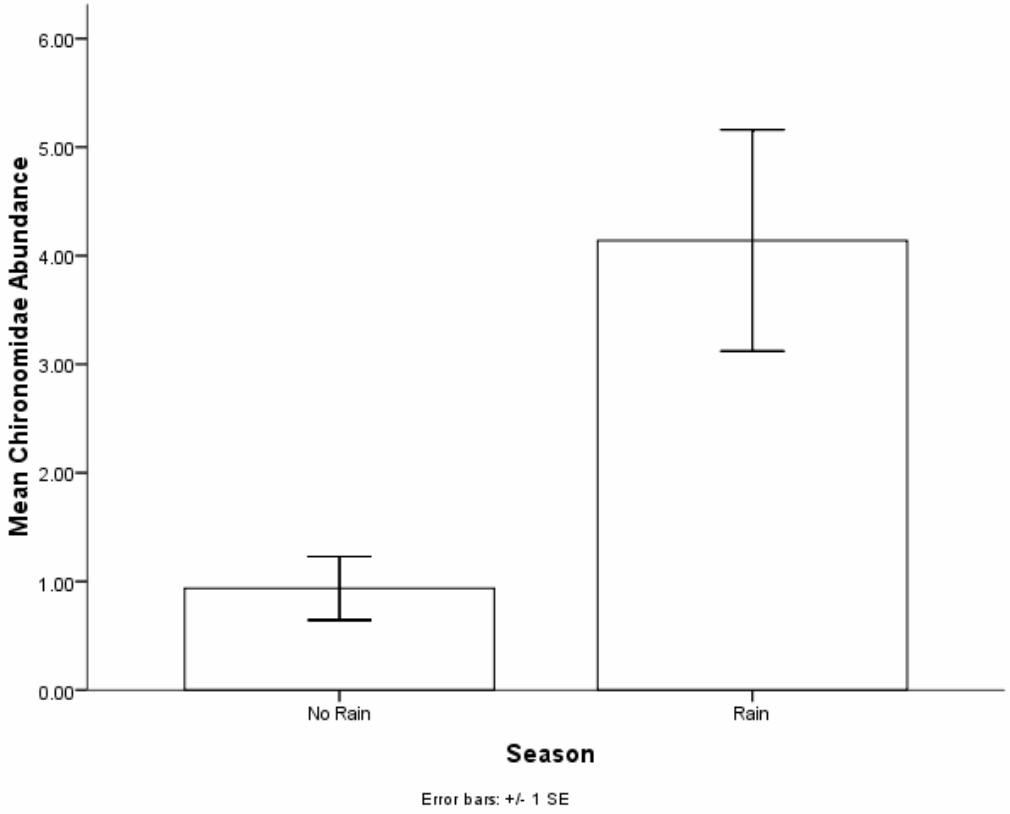
As the abundance data for the analysed families were not normally distributed and only the distribution of Cecidomyiidae could be transformed into a normal distribution, all non transformed family data were analysed using non parametric procedures. As before all significant and no significant interactions are summarised in table 4.2 at the end of the section.

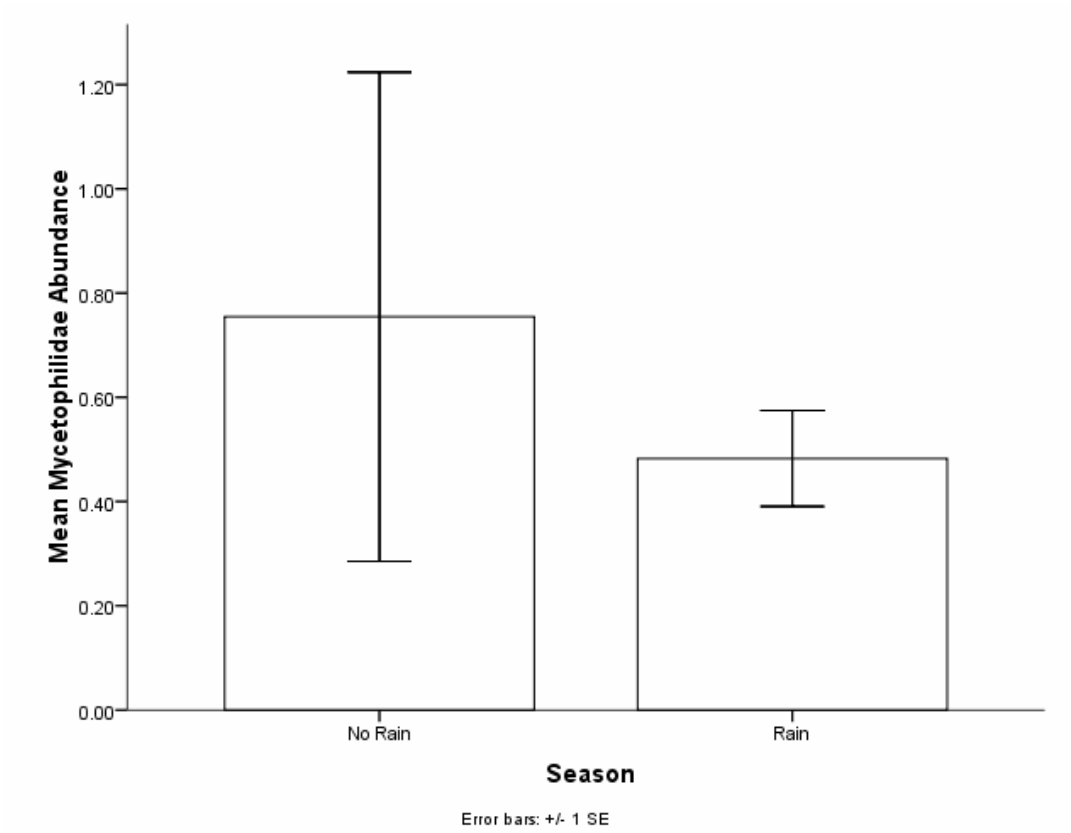
Before investigating how each of the nematoceran families was affected by height classes across the two environmental conditions, periods of rain and no rain were compared. All families showed a significant difference in rank with Sciaridae, $z = -7.78$, $p < 0.001$, Ceratopogonidae, $z = -4.78$, $p < 0.001$, Chironomidae, $z = -5.48$, $p < 0.001$, and

Cecidomyiidae, $z = -3.12$, $p < 0.005$, all showing significantly higher abundance during the rains. However Mycetophilidae showed a significantly higher abundance during periods of no rain, $z = -3.16$, $p < 0.005$. Figure 4.5, illustrates these differences.




Mean Ceratopogonidae Abundance
2.50
2.00
1.50
1.00
0.50
0.00
No Rain
Rain
Season
Error bars: +/- 1 SE


Mean Chironomidae Abundance
6.00
5.00
4.00
3.00
2.00
1.00
0.00
No Rain
Rain
Season
Error bars: +/- 1 SE



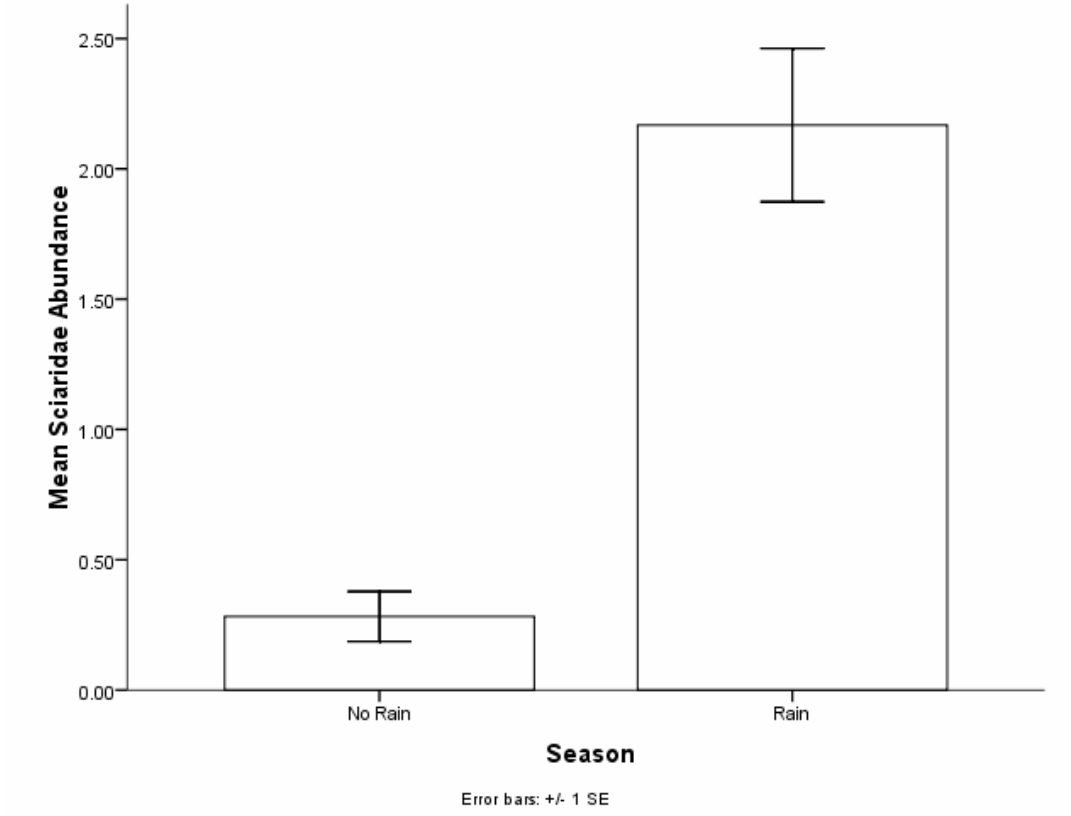


Fig 4.5 Differences in nematoceran family abundance (per trap day) between periods of rain and no rain, Kwano forest.

To investigate how dipteran abundance differed between height classes the data were split by rain and no rain. During periods of no rain Sciaridae (H = 0.06, df = 2, *ns*), Mycetophilidae (H = 0.19, df =2, *ns*) and Chironomidae (H = 0.99, df = 2, *ns*) showed no significant differences between height classes within the canopy. However both Ceratopogonidae (H = 6.10, df = 2, p <0.05) and Cecidomyiidae (H = 21.86, df = 2, p < 0.001) did show significant differences. Therefore only the Ceratopogonidae and Cecidomyiidae were taken forward to Mann-Whitney post hoc analysis with Bonferroni corrections.

The post hoc results showed that after Bonferroni corrections the Ceratopogonidae showed no significant differences between height classes during periods of no rain. Whereas the Cecidomyiidae did show significantly higher abundance in the ground compared to the mid canopy, z = -3.77, p < 0.001, ground to high canopy, z = -4.33, p < 0.001, but not between mid and high canopy samples, z = -0.64, *ns*.

During periods of rain the Kruskal-Wallis test showed that Ceratopogonidae (H = 10.49, df = 2, p = 0.005) and Sciaridae (H = 9.51, df = 2, p <0.05) had significant differences in abundance between the three height classes. Mycetophilidae (H = 5.67, df = 2, *ns*), Chironomidae (H = 5.78, df = 2, *ns*) and Cecidomyiidae (H = 0.32, df = 2, *ns*) showed no significant difference in abundance across the three height classes.

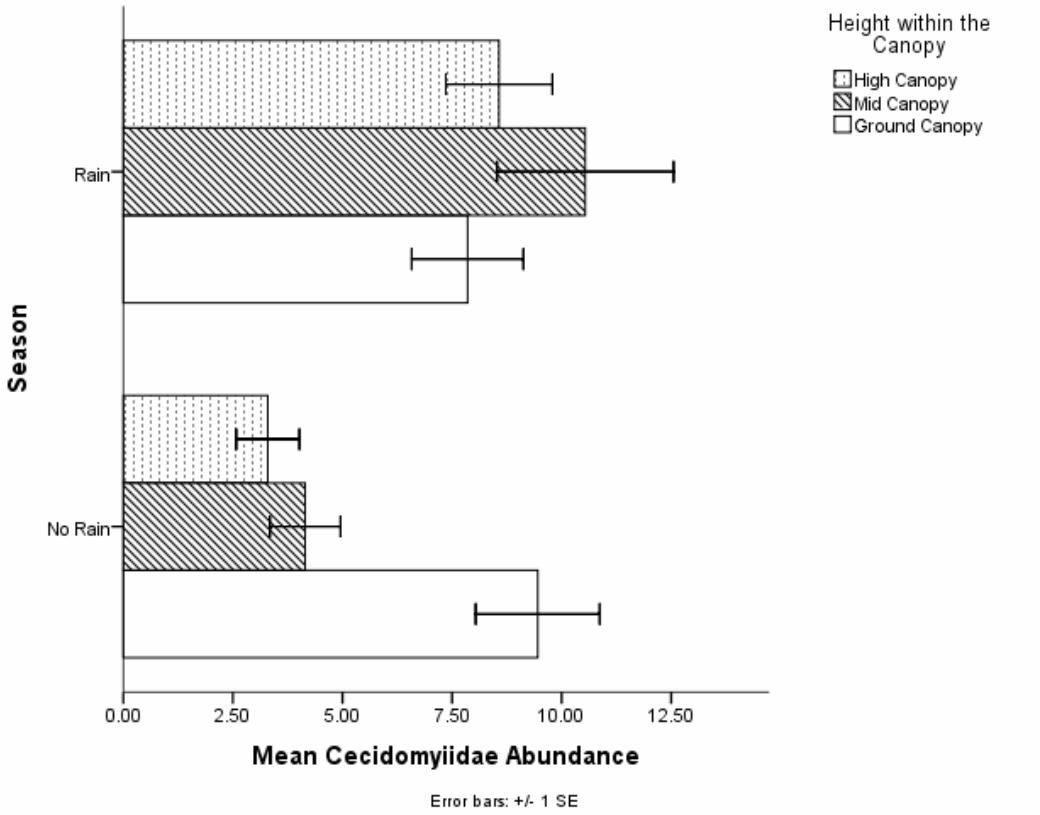
As before only families that showed significant results in the Kruskal-Wallis tests were taken forward to post hoc analysis with a corrected p value of 0.016. The Ceratopogonidae showed significantly higher abundance in the mid canopy than the ground canopy, z = -3.156, p < 0.016, but there was no significant difference between the ground canopy and high canopy or the high canopy and the mid canopy after Bonferroni correction. Sciaridae abundance was significantly higher in the high canopy when compared to the ground

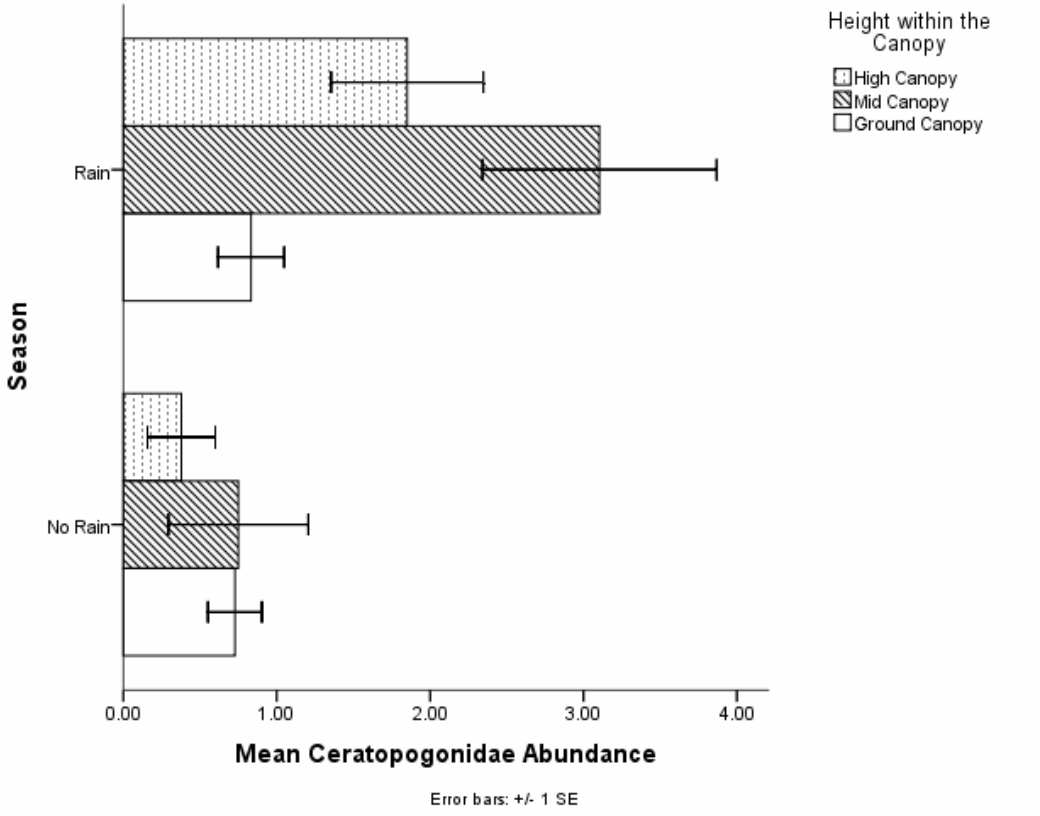
canopy, z = -3.02, $p < 0.005$, but there was no significant difference between ground and mid canopy or mid and high canopy.

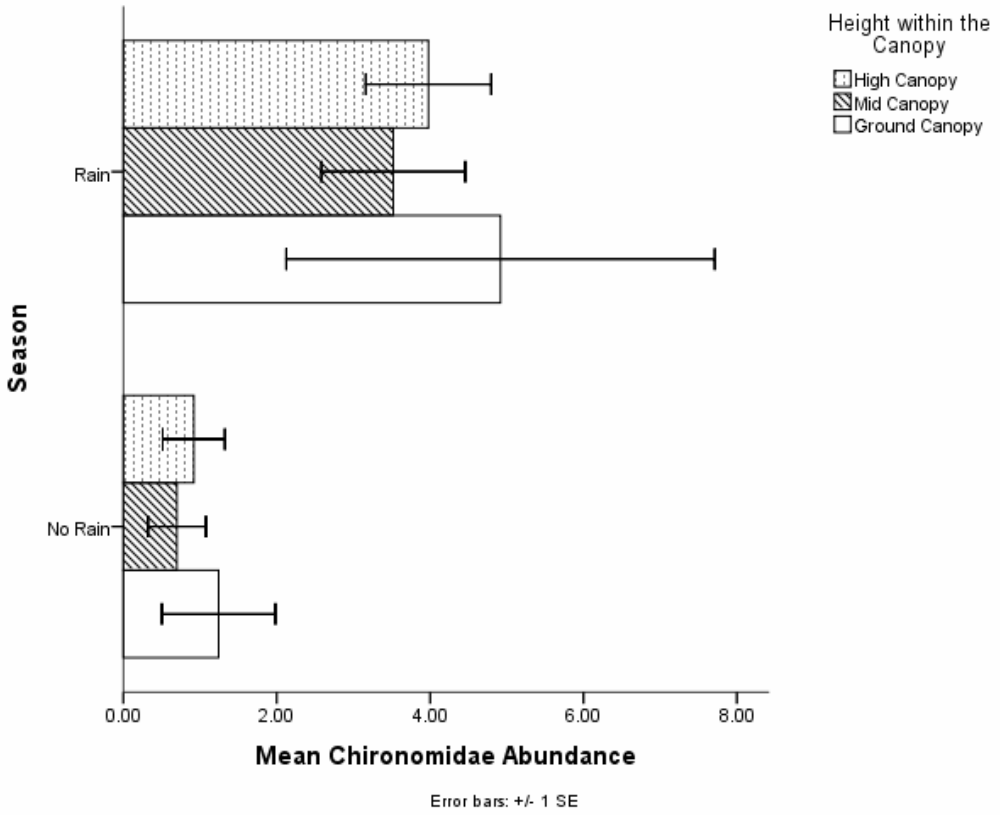
To test for differences within heights across periods of rain and no rain, a further Kruskal-Wallis test was performed, this time with the data split between height classes with presence or absence of rain as the independent factor. Sciaridae showed a significant increase in ground canopy abundance during periods of rain (H = 13.47, df = 1, $p < 0.001$) as did Mycetophilidae (H = 6.08, df = 1, $p < 0.05$). No other family showed any significant difference in ground canopy abundance between the two environmental conditions.

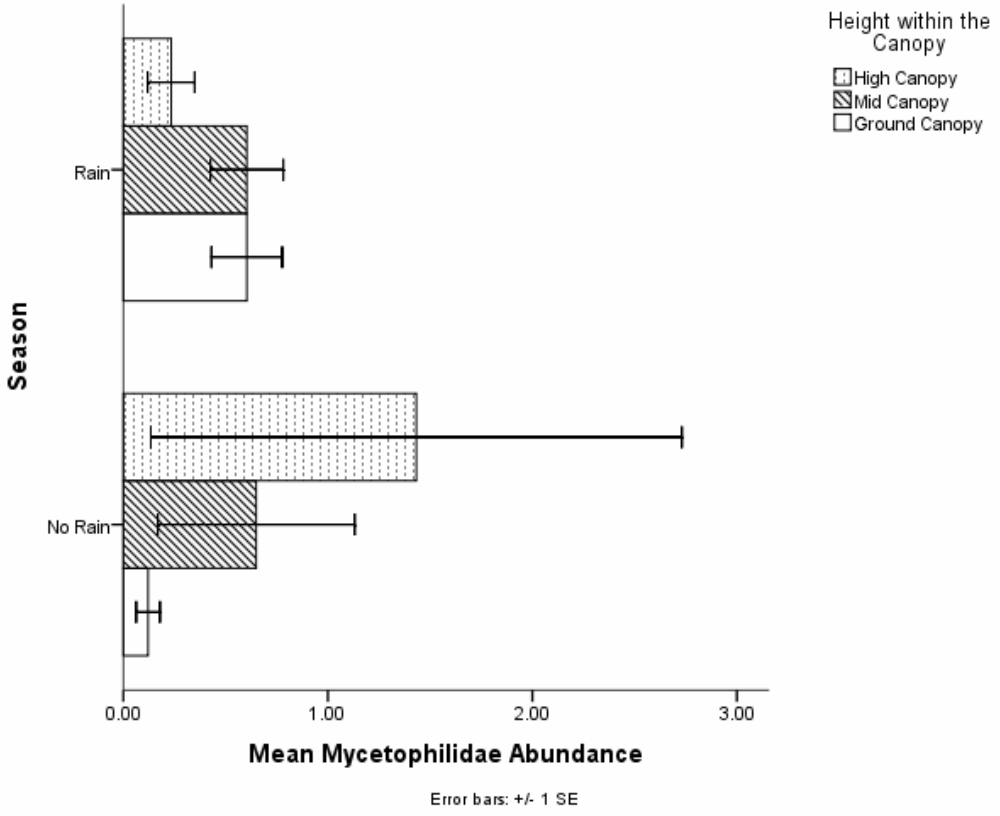
All families showed significant differences in mid canopy abundance between periods of rain and no rain with Sciaridae (H = 22, df = 1, $p < 0.001$), Ceratopogonidae (H = 17.91, df = 1, $p < 0.001$), Cecidomyiidae (H = 6.61, df = 1, $p < 0.05$) and Chironomidae (H = 13.2, df = 1, $p < 0.001$), all significantly increasing abundance during the rains. Although Mycetophilidae abundance appears to be equal between the two seasons (see fig 4.6), the ranked effect showed periods of rain to be significantly higher ranked than periods of no rain (H = 4.1, df = 1, $p <0.05$).

Only the Mycetophilidae showed no significant difference in abundance in the high canopy (H = 0.74, df = 1, *ns*), where as Sciaridae (H = 26.6, df = 1, $p < 0.001$), Ceratopogonidae (H = 15.36, df = 1, $p < 0.001$), Cecidomyiidae (H = 13.10, df = 1, $p < 0.001$) and Chironomidae (H = 16.03, df = 1, $p < 0.001$), all showed an increase in abundance during periods of rain. Figure 4.6, below illustrates how the abundance of these families changes between canopy heights and periods of rain and no rain within the Kwano forest.


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
0.00
2.50
5.00
7.50
10.00
12.50
Mean Cecidomyiidae Abundance
Error bars: +/- 1 SE


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
0.00
1.00
2.00
3.00
4.00
Mean Ceratopogonidae Abundance
Error bars: +/- 1 SE


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
0.00
2.00
4.00
6.00
8.00
Mean Chironomidae Abundance
Error bars: +/- 1 SE


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
0.00
1.00
2.00
3.00
Mean Mycetophilidae Abundance
Error bars: +/- 1 SE

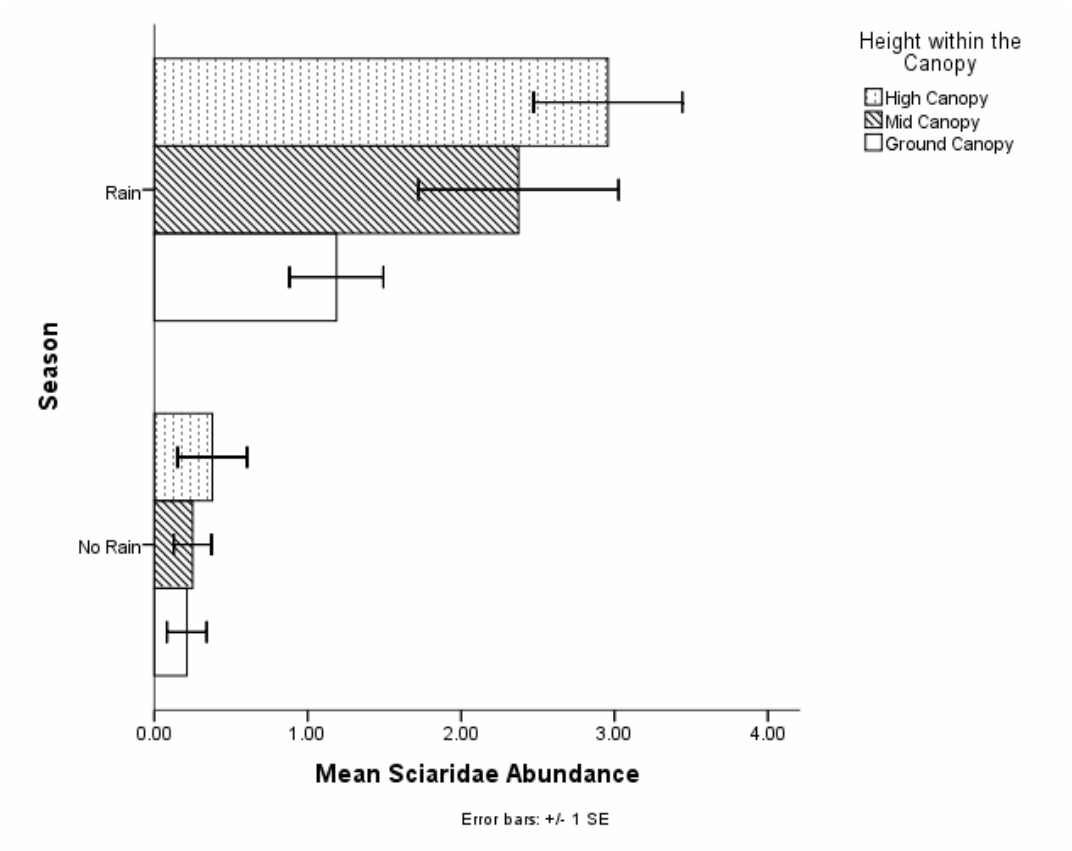


Fig 4.6 Nematocera family abundance (per trap day) at ground, mid and high canopy levels within periods of rain and no rain, Kwano forest.

Table 4.2. Summary of interactions of Nematocera families to height and season, match each column to a row to see if there is a significant difference (*) or non significant difference (*ns*) between factors, see fig 4.6, above, for magnitude and direction of effect.

Cecidomyiidae Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*ns*	*		*	
Ground Wet			*ns*			*ns*		*ns*
Mid Dry			*			*	*ns*	
Mid Wet				*ns*	*			*ns*
High Dry			*		*ns*			*
High Wet				*ns*		*ns*	*	

Ceratopogonidae Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*ns*	ns		ns	
Ground Wet			*ns*			*		*ns*
Mid Dry			ns			*	*ns*	
Mid Wet				*	*			*ns*
High Dry			ns		*ns*			*
High Wet				*ns*		*ns*	*	

Sciaridae Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*	ns		ns	
Ground Wet			*			*ns*		*
Mid Dry			ns			*	*ns*	
Mid Wet					*			
High Dry			ns		*ns*			*
High Wet				*		*ns*	*	

Mycetophilidae Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*	ns		ns	
Ground Wet			*			*ns*		*ns*
Mid Dry			ns			*	*ns*	
Mid Wet				*ns*	*			
High Dry			ns		*ns*			ns
High Wet				*ns*		*ns*	ns	

Chironomidae Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*ns*	ns		ns	
Ground Wet			*ns*			*ns*		*ns*
Mid Dry			ns			*	*ns*	
Mid Wet				*ns*	*			*ns*
High Dry			ns		*ns*			*
High Wet				*ns*		*ns*	*	

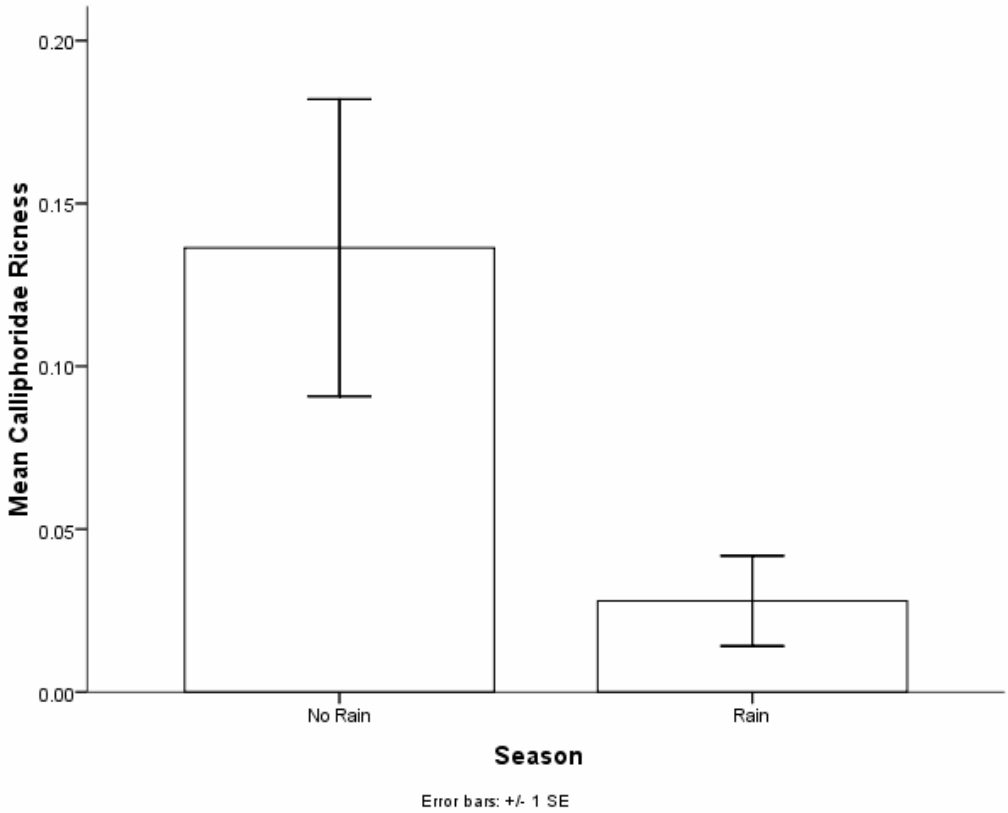
4.3.5 Analysis of the Calyptrates

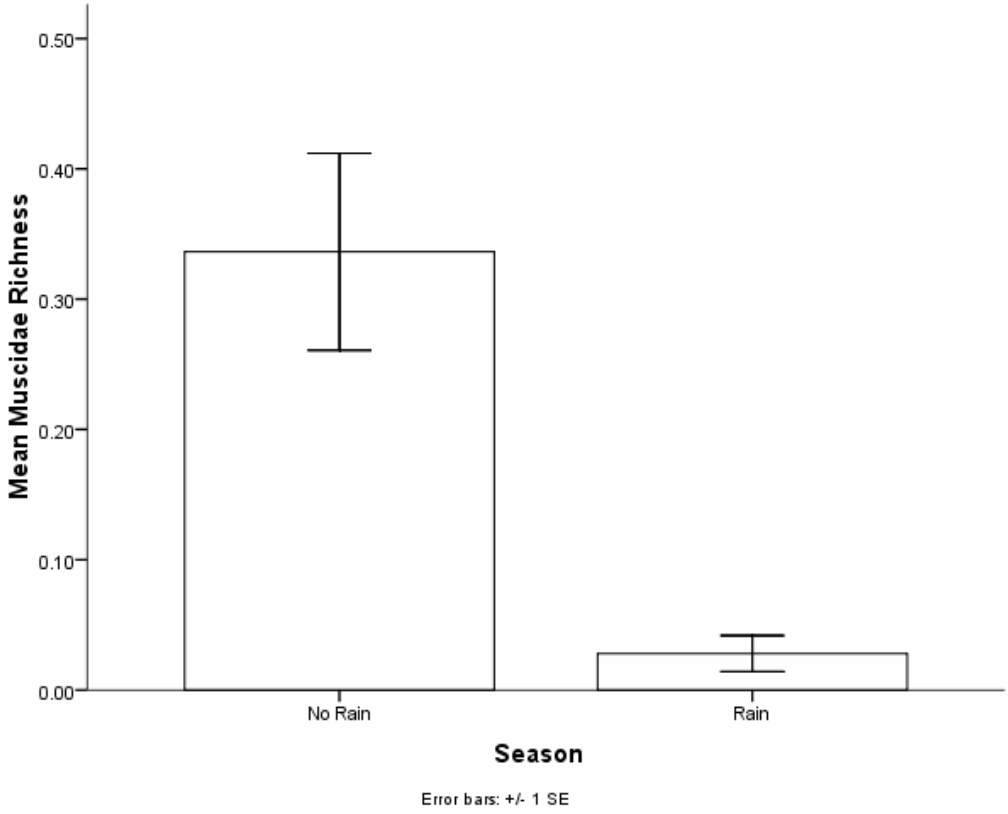
Section 4.3.3 showed that Calyptrates are significantly affected by both height and season; therefore here the analysis will be taken further. A total 213 individuals identified to eight families, 32 genera and 45 species were collected across all samples. This taxanomic

group represents the smallest contribution to overall abundance (4.7 % of total Diptera abundance); however the families contribution to ecological services, such as nutrient cycling, is well documented and other than the Nematocera this is the only other group to be affected by rainfall within the Kwano forest. Section 4.3.3 showed that Calyptrates are negatively affected by rainfall and that there are significant differences in the abundance distribution throughout the vertical column (See fig. 4.4 and fig. 4.5 for details).

Richness data were generated for each of the families identified within the group. The data were not normally distributed and transformation did not create a normal distribution; therefore the untransformed data were analysed using non parametric Kruskal-Wallis and Mann-Whitney tests with Bonferroni corrections where necessary. Four families contributed the majority of the richness within the group, these were; Tachinidae, Calliphoridae, Sarcophagidae and Muscidae. The other families, Glossinidae, Rhiniidae, Lemoniidae and Tephritidae contained too few individuals (< 10) for analysis.

The results of the analysis showed that Tachinidae, $z = -2.10$, $p < 0.05$, Calliphoridae, $z = -2.20$, $p < 0.05$, Sarcophagidae, $z = -4.517$, $p < 0.001$ and Muscidae, $z = -4.52$, $p < 0.001$, all had significantly higher richness during periods of no rain. Figure 4.7, below illustrates the magnitude of these differences.


Mean Calliphoridae Ricness
0.20
0.15
0.10
0.05
0.00
No Rain
Rain
Season
Error bars: +/- 1 SE


Mean Muscidae Richness
0.50
0.40
0.30
0.20
0.10
0.00
No Rain
Rain
Season
Error bars: +/- 1 SE

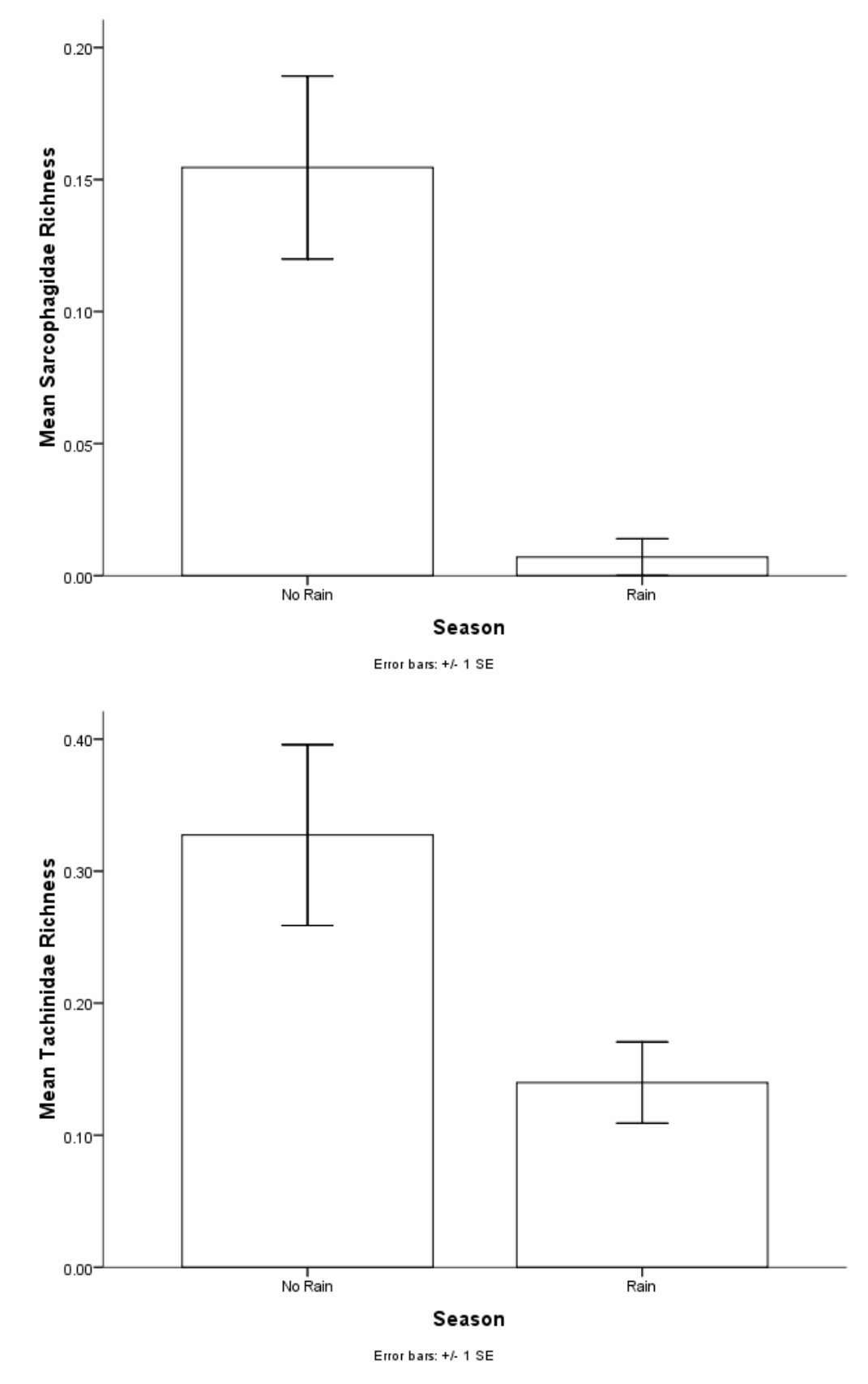
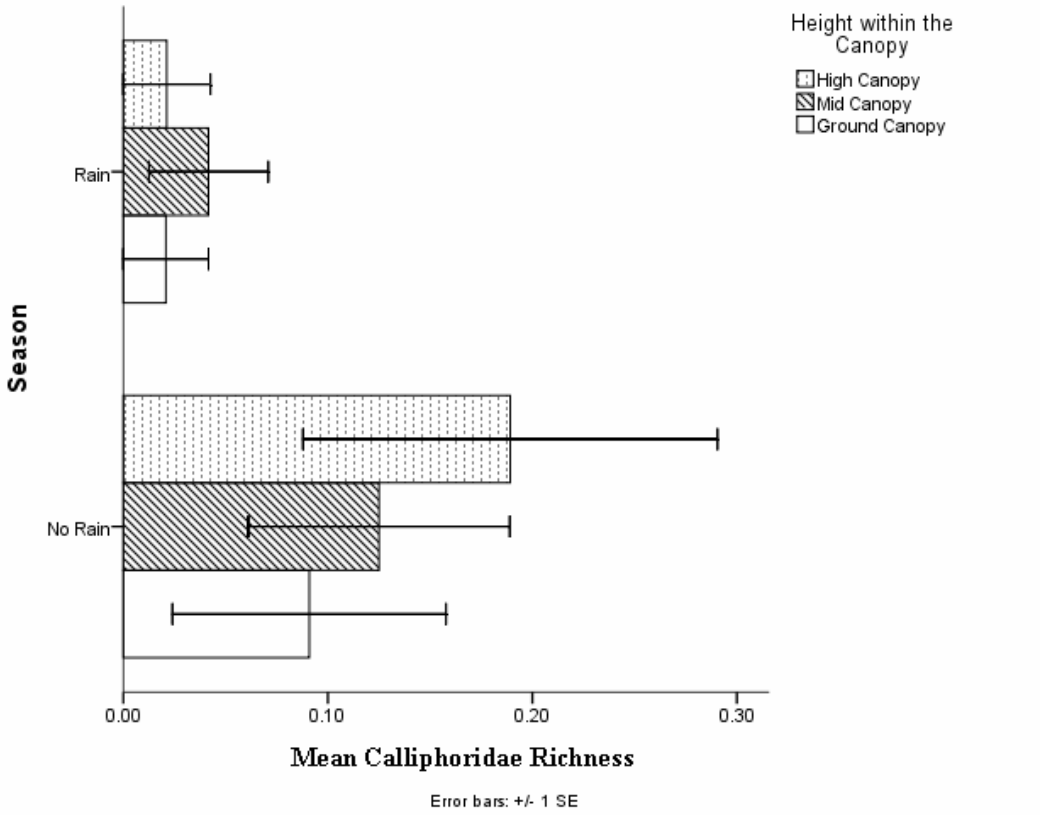
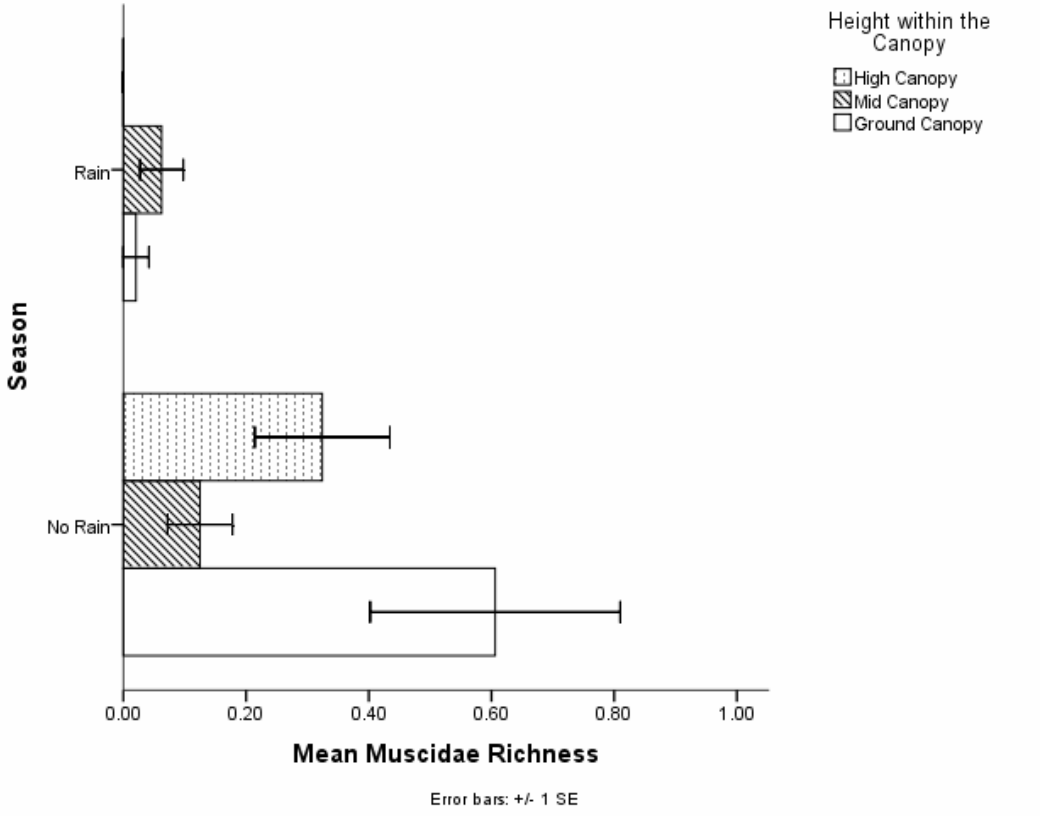


Fig. 4.7. Tachinidae, Muscidae, Saecophagidae and Calliphoridae richness (per trap day) during periods of rain and no rain, Kwano forest.

The data were then split between periods of rain and no rain in SPSS 17 to investigate potential differences in richness within each of the height classes. Tachinidae ($H = 2.70$, $df = 2$, *ns*), Calliphoridae ($H = 0.54$, $df = 2$, *ns*), Sarcophagidae ($H = 4.42$, $df = 2$, *ns*) and Muscidae ($H = 3.42$, $df = 2$, *ns*) all showed no overall significance within the data sets for periods of no rain. During periods of rain Tachinidae ($H = 3.12$, $df = 2$, *ns*), Calliphoridae ($H = 0.50$, $df = 2$, *ns*), Sarcophagidae ($H = 2.04$, $df = 2$, *ns*) and Muscidae ($H = 3.52$, $df = 2$, *ns*) again showed no overall significance within the data set.

The richness data were then split by height class to look for differences in richness between periods of rain and no rain within each of the height classes. The ground canopy samples showed that Tachinidae, $z = -2.96$, $p < 0.005$, and Muscidae, $z = -3.41$, $p = 0.001$, had higher richness during periods of no rain, where as the Sarcophagidae, $z = -1.72$, *ns*, and Calliphoridae, $z = 0.94$, *ns*, showed no significant difference in richness between rain and no rain periods. Neither the Tachinidae, $z = -0.15$, *ns*, Calliphoridae, $z = -1.09$, *ns*, nor Muscidae, $z = -1.01$, *ns*, showed any significant difference in richness between rain and no rain periods in the mid canopy samples. Whereas the Sarcophagidae did show a significantly higher richness in the mid canopy, $z = -2.76$, $p < 0.01$. Tachinidae, $z = -0.873$, *ns*, and Calliphoridae, $z = -1.68$, *ns*, showed no significant difference in richness between periods of rain and no rain within the high canopy; whereas Sarcophagidae, $z = -3.10$, $p < 0.01$, and Muscidae, $z = -3.33$, $p = 0.001$, showed a significant decrease from periods of no rain to rain. Figure 4.8, below illustrates these differences and table 4.3 summarises the results.


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
0.00
0.10
0.20
0.30
Mean Calliphoridae Richness
Error bars: +/- 1 SE


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
0.00
0.20
0.40
0.60
0.80
1.00
Mean Muscidae Richness
Error bars: +/- 1 SE

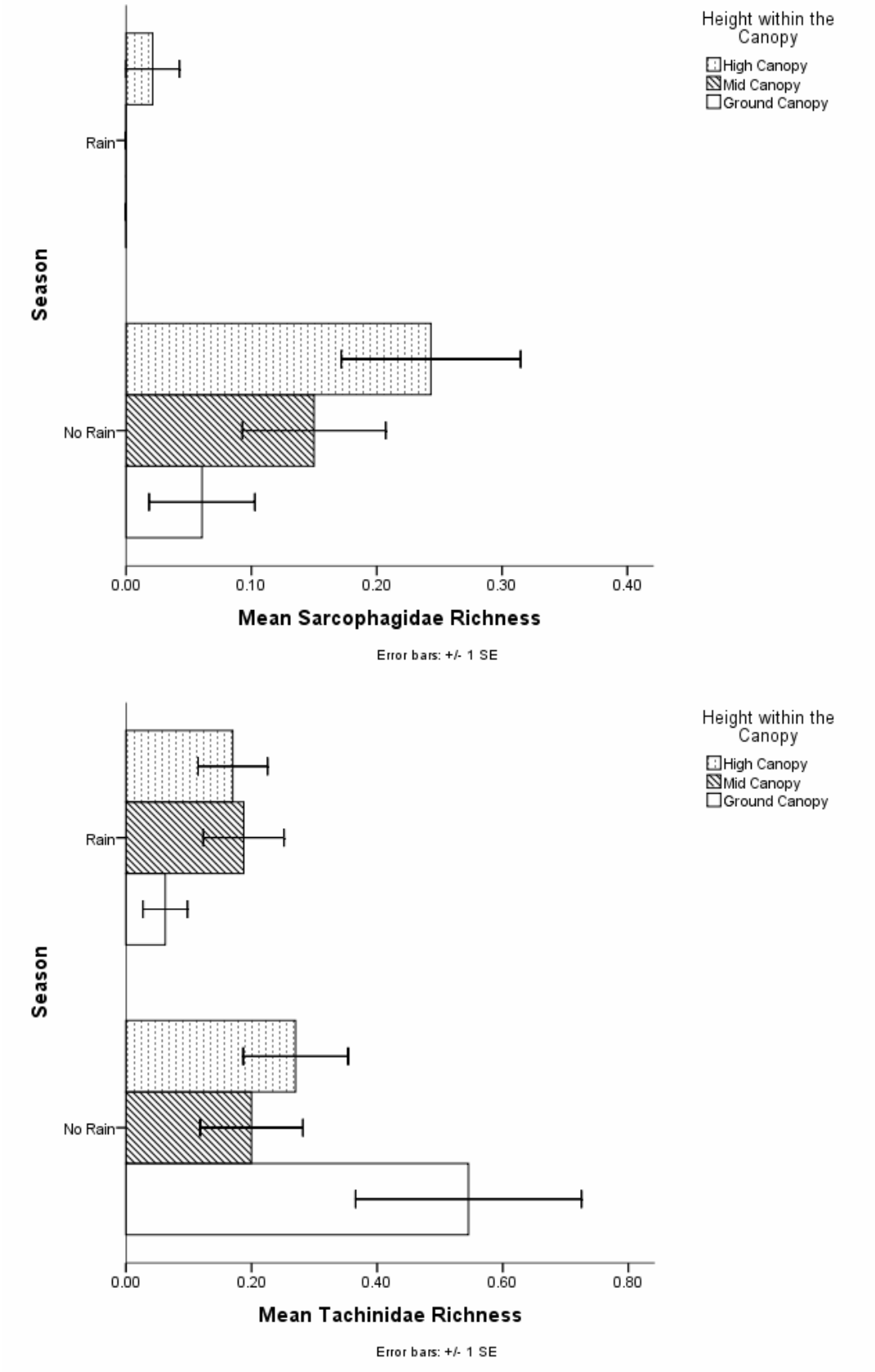


Fig 4.8.. Differences in richness (per trap day) within height classes between periods of rain and no rain in Calliphoridae, Tachinidae and Muscidae, Kwano forest.

Table 4.3. Summary of interactions of Calyptrate family richness to height and season, match each column to a row to see if there is a significant difference (*) or non significant difference (*ns*) between factors, see fig 4.8. above, for magnitude and direction of effect.

Calliphoridae Richness

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*ns*	*ns*		*ns*	
Ground Wet			*ns*			*ns*		*ns*
Mid Dry			*ns*			*ns*	*ns*	
Mid Wet				*ns*	*ns*			*ns*
High Dry			*ns*		*ns*			*ns*
High Wet				*ns*		*ns*	*ns*	

Muscidae Richness

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*	*ns*		*ns*	
Ground Wet			*			*ns*		*ns*
Mid Dry			*ns*			*ns*	*ns*	
Mid Wet				*ns*	*ns*			*ns*
High Dry			*ns*		*ns*			*
High Wet				*ns*		*ns*	*	

Tachinidae Richness

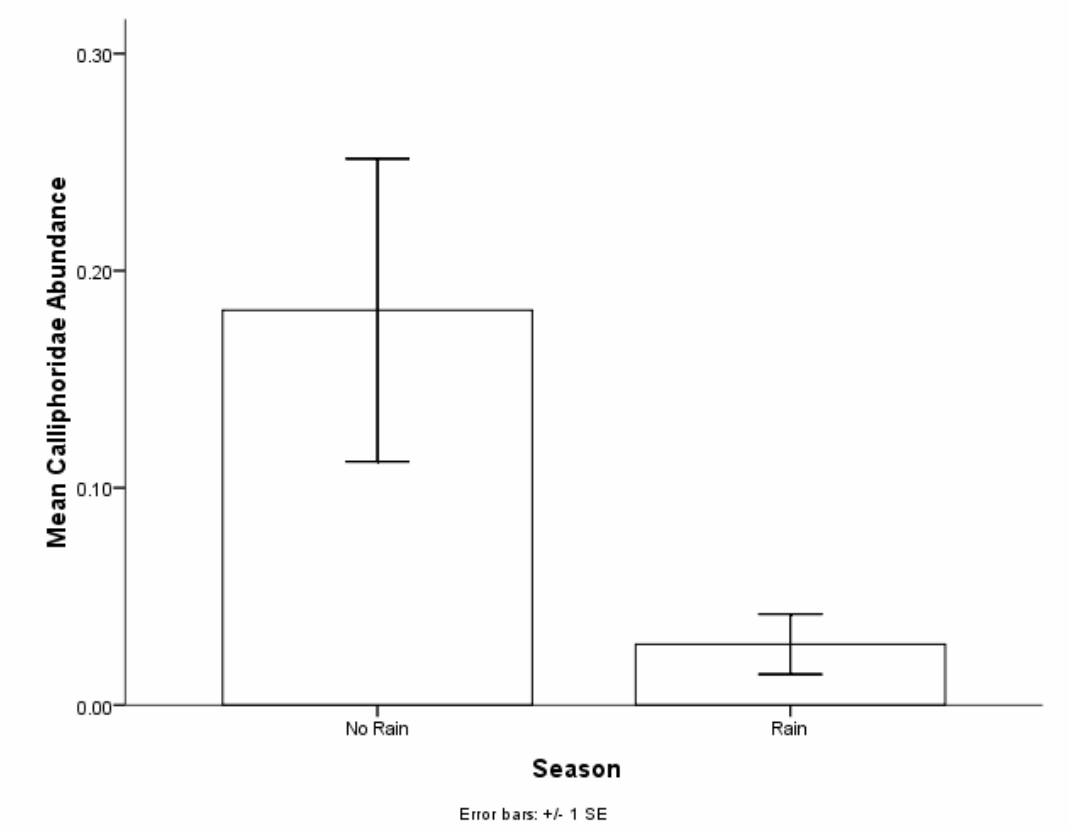
	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*	*ns*		*ns*	
Ground Wet			*			*ns*		*ns*
Mid Dry			*ns*			*ns*	*ns*	
Mid Wet				*ns*	*ns*			*ns*
High Dry			*ns*		*ns*			*ns*
High Wet				*ns*		*ns*	*ns*	

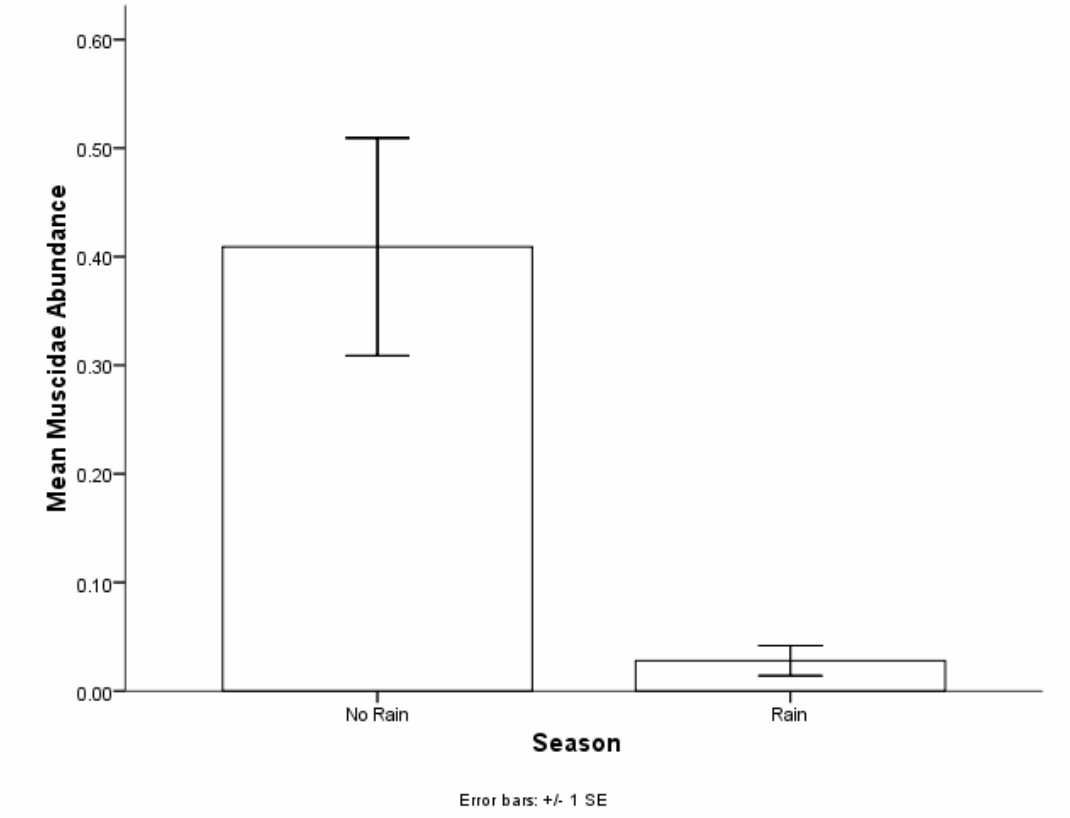
Sarcophagidae Richness

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*ns*	*ns*		*ns*	
Ground Wet			*ns*			*ns*		*ns*
Mid Dry			*ns*			*	*ns*	
Mid Wet				*ns*	*			*ns*
High Dry			*ns*		*ns*			*
High Wet				*ns*		*ns*	*	

Analysis was now performed on the overall abundance of the Calyptrate families. Abundance data were again not normally distributed; therefore analysis followed the same procedure as previously in this chapter. Initial comparison of seasonal differences in the four families abundance showed that Sacrophagidae, $z = -4.41$, $p < 0.001$, Muscidae, $z = -4.36$, $p < 0.001$, Tachinidae, $z = -2.08$, $p < 0.05$, and Calliphopidae, $z = -2.21$, $p < 0.05$, all

showed significantly higher abundance in periods of no rain than in periods of rain. Figure 4.9, illustrates the magnitude of these differences.





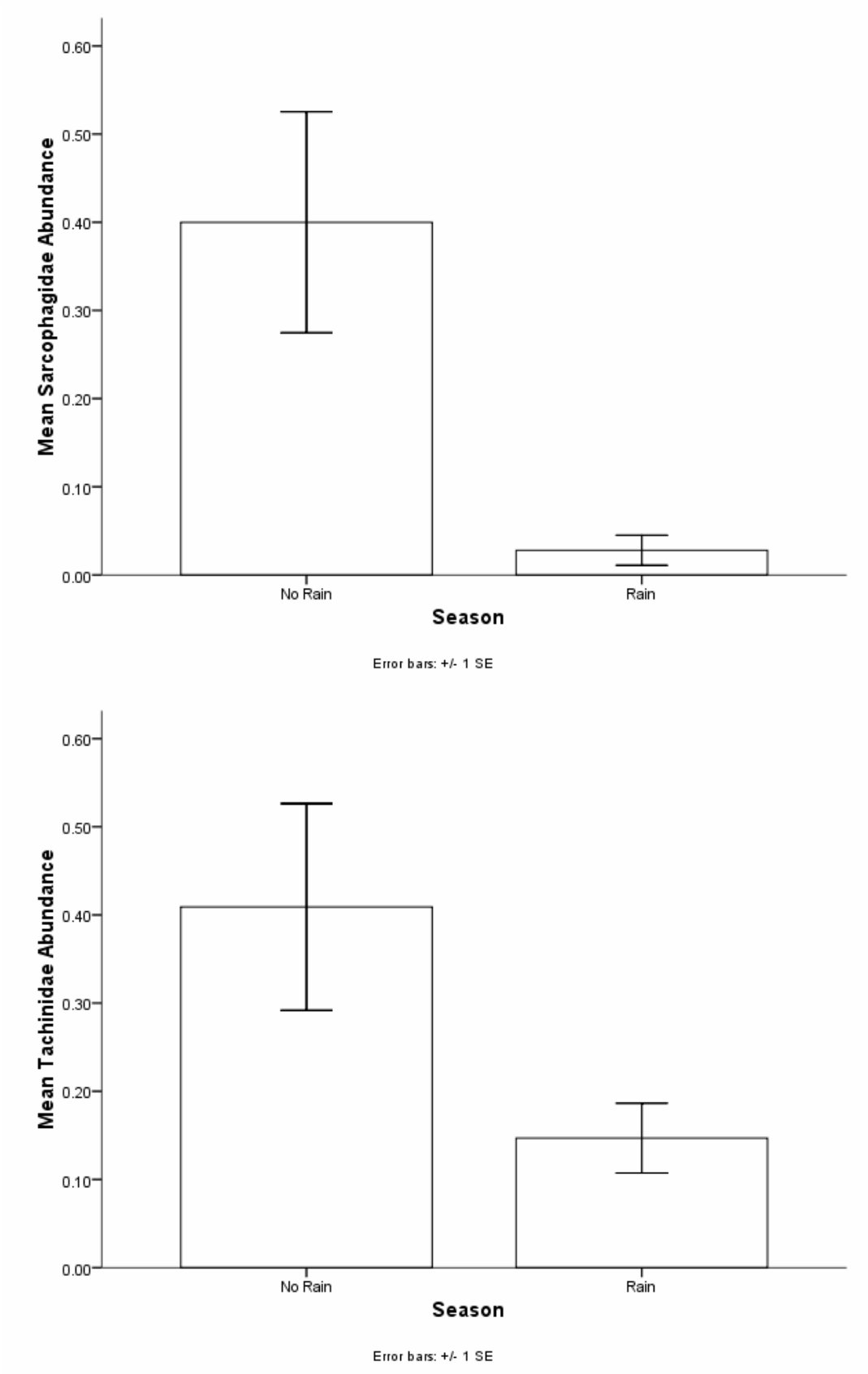
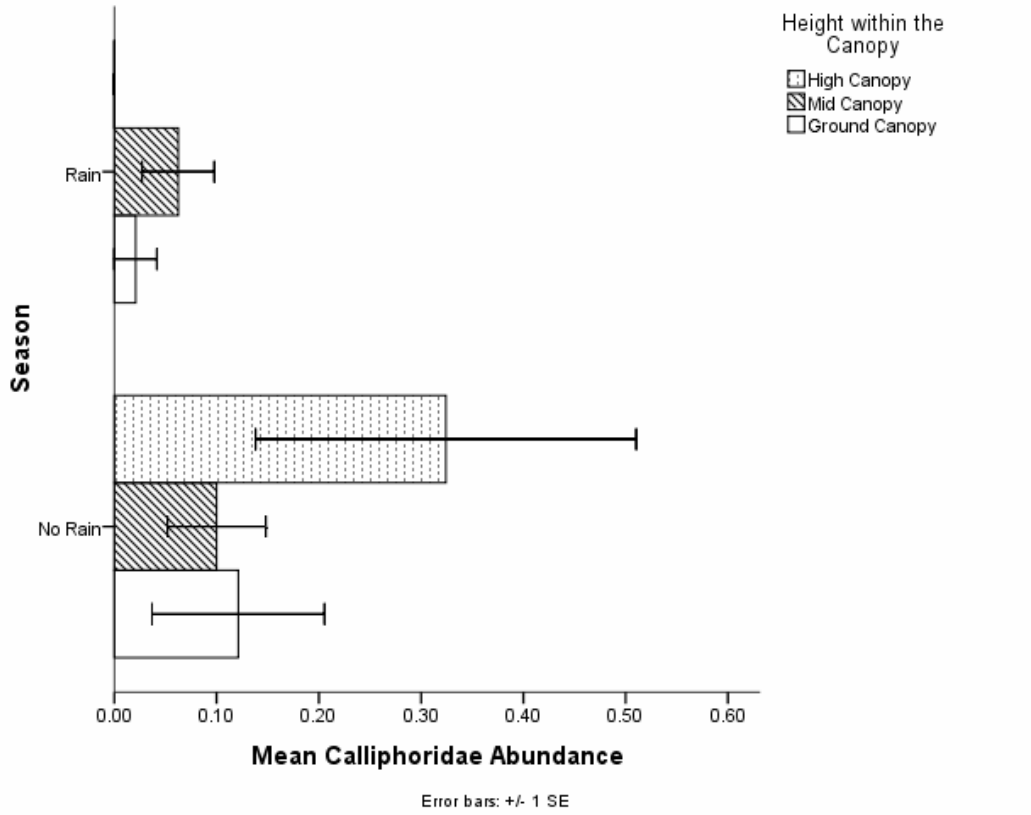
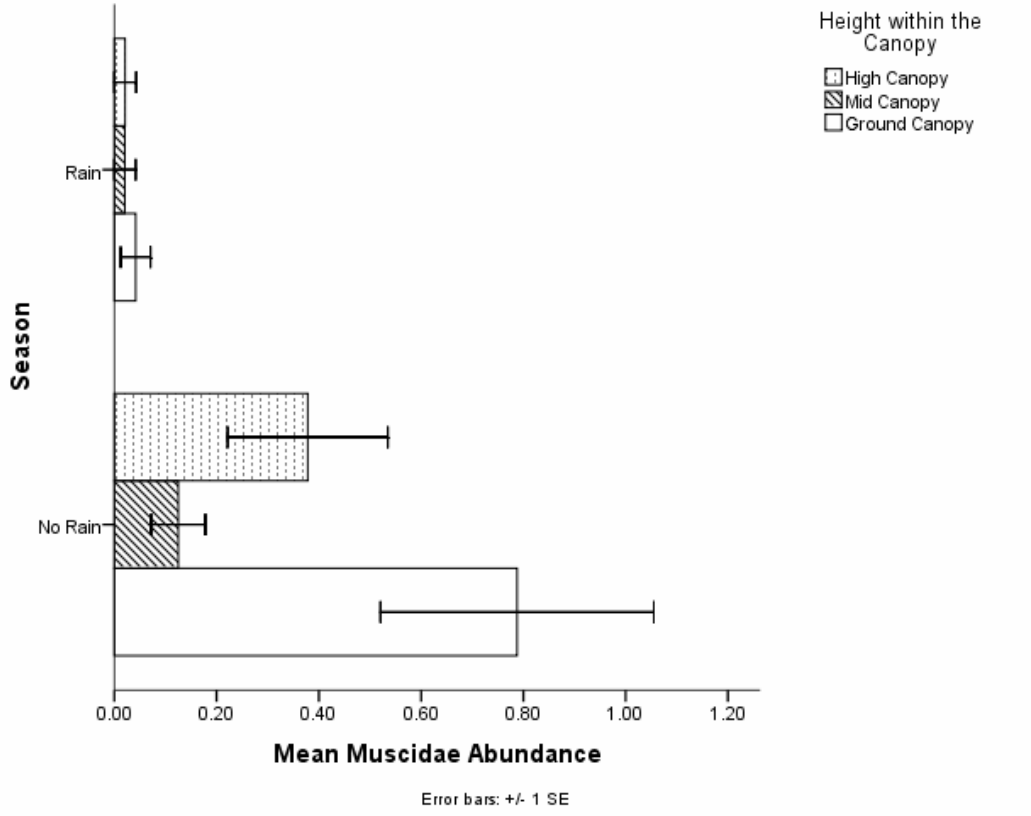


Fig 4.9. Differences in season abundances (per trap day) of four Calyptrate families.

The results of the Kruskal-Wallis test showed that in neither periods of rain or no rain was there any significant difference in abundance across the three height classes (see table 4.4 for clarification). Therefore no post hoc analysis was conducted on these results. The data were rearranged to test for differences in abundances between periods of rain and no rain, within the height classes. The results showed that at ground level both Muscidae, $z = -3.3$, $p = 0.001$, and Tachinidae, $z = -3.3$, $p = 0.001$, showed significantly higher abundances during periods of no rain. Whereas the Sarcophagidae, $z = -1.83$, *ns*, and Calliphoridae, $z = 0.96$, *ns* showed no statistical differences between seasons in the ground canopy. In the mid canopy only Sarcophagidae, $z = -3.00$, $p < 0.005$, showed significantly higher abundances during periods of no rain. Whereas Muscidae, $z = -1.92$, *ns*, Tachinidae, $z = -0.58$, *ns*, and Calliphoridae, $z = -0.64$, *ns*, showed no seasonal difference at the mid canopy level. Tachinidae, $z = -0.86$, *ns*, did not show any significant differences between periods of rain and no rain in the high canopy. However, Sarcophagidae, $z = -2.71$, $p < 0.01$, Muscidae, $z = -2.35$, $p < 0.05$, and Calliphoridae, $z = -2.30$, $p < 0.05$, all showed significantly higher abundances during periods of no rain within the high canopy. Figure 4.10, below illustrates the magnitude of these differences.


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
0.00
0.10
0.20
0.30
0.40
0.50
0.60
Mean Calliphoridae Abundance
Error bars: +/- 1 SE


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
0.00
0.20
0.40
0.60
0.80
1.00
1.20
Mean Muscidae Abundance
Error bars: +/- 1 SE

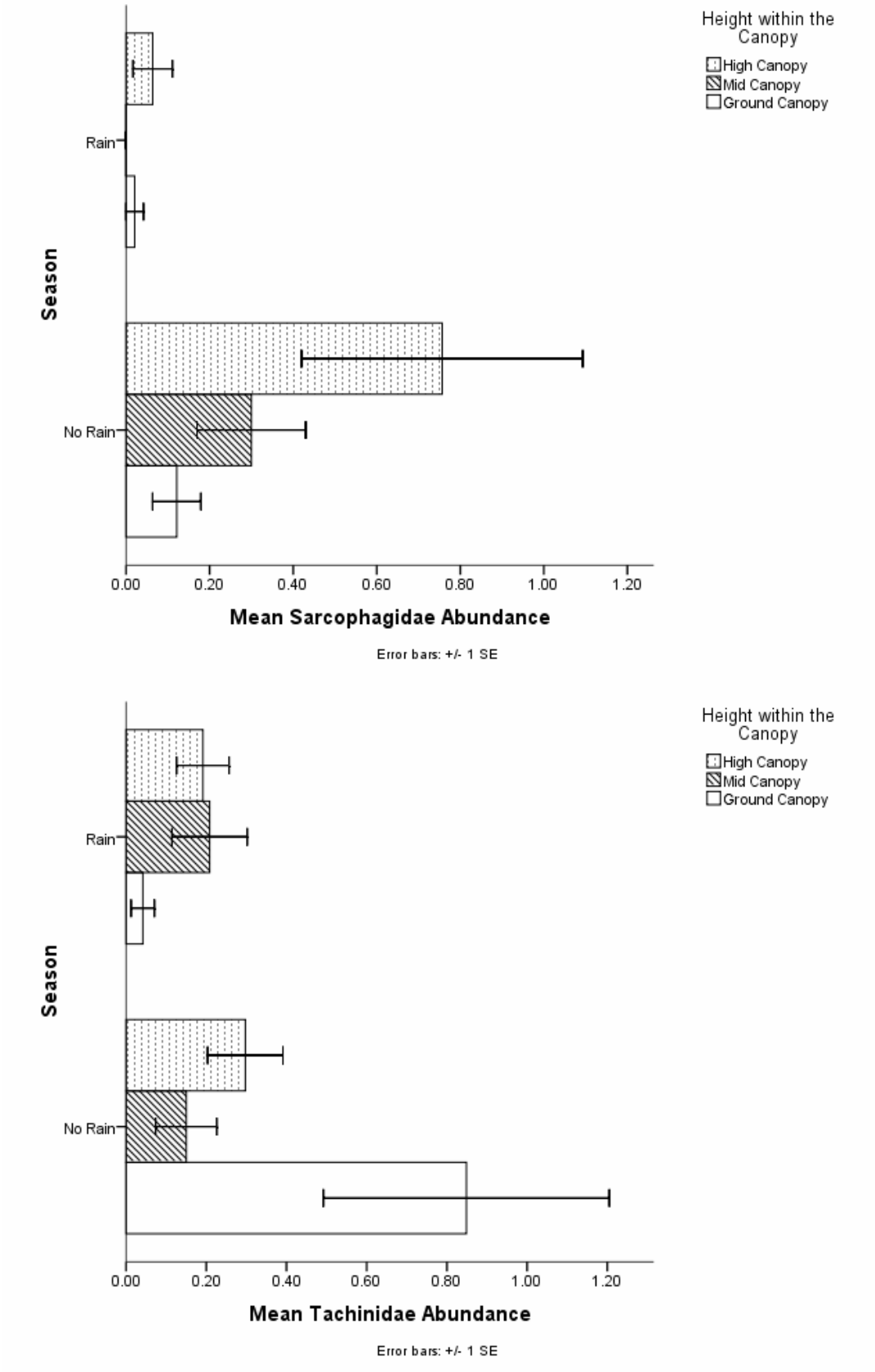


Fig 4.10. Differences in abundances (per trap day) between height categories and periods of rain and no rain in four Calyptrate families, Kwano forest.

Table 4.4. Summary of interactions of Calyptrate family abundance to height and season, match each column to a row to see if there is a significant difference (*) or non significant difference (*ns*) between factors, see fig 4.10, above, for magnitude and direction of effect.

Calliphoridae Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*ns*	*ns*		*ns*	
Ground Wet			*ns*			*ns*		*ns*
Mid Dry			*ns*			*ns*	*ns*	
Mid Wet				*ns*	*ns*			*ns*
High Dry			*ns*		*ns*			*
High Wet				*ns*		*ns*	*	

Muscidae Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*	*ns*		*ns*	
Ground Wet			*			*ns*		*ns*
Mid Dry			*ns*			*ns*	*ns*	
Mid Wet				*ns*	*ns*			*ns*
High Dry			*ns*		*ns*			*
High Wet				*ns*		*ns*	*	

Tachinidae Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*	*ns*		*ns*	
Ground Wet			*			*ns*		*ns*
Mid Dry			*ns*			*ns*	*ns*	
Mid Wet				*ns*	*ns*			*ns*
High Dry			*ns*		*ns*			*ns*
High Wet				*ns*		*ns*	*ns*	

Sarcophagidae Abundance

	Rain	No rain	Ground Dry	Ground Wet	Mid Dry	Mid Wet	High Dry	High Wet
Rain		*						
No Rain	*							
Ground Dry				*ns*	*ns*		*ns*	
Ground Wet			*ns*			*ns*		*ns*
Mid Dry			*ns*			*	*ns*	
Mid Wet				*ns*	*			*ns*
High Dry			*ns*		*ns*			*
High Wet				*ns*		*ns*	*	

4.4 Conclusions

The perception of a clear set of defined structural canopy strata is a misconception that has been hard to dispel (see Richards (1952) for an example of historical viewpoint). Generalisations of how the structure of the canopy follows predetermined rules governed by height are now thought to underestimate the true complexity of this forest system both in an environmental and ecological context (Parker and Brown, 2000). Accepting the concept that vertical stratification is akin to edge effects is a way of defining the phenomena and placing it within the forest system. The concept of a dorsal edge to the canopy creates a template by which we can start to piece together information and begin to understand the nature and role that the vertical column plays within a functioning forest ecosystem (Foggo et al., 2001, Ozanne et al., 2003).

Through research into edge effects, abiotic factors such as variations in temperature, humidity, direct sunlight and exposure to precipitation have been shown to influence the structure, density and complexity of both floral and faunal populations at the forest edge and through into the interior (Bierregaard et al., 1992, Laurance et al., 2002). These variations in microclimate along the lateral gradient of the forest floor are known to reduce temperature and increase humidity from the forest edge into the interior (Marsh, 2003). This pattern of environmental change has also been shown by the results of this study. Although the dry season results showed no significant differences in microclimate from the high to the ground canopy, the wet season results showed that there is a clear aggregation in both temperature and humidity within the vertical column. This stratification was exactly what one would expect to find if investigating a lateral edge effect, with temperature significantly higher towards the high canopy (dorsal edge) and humidity significantly higher towards the ground canopy and forest floor (interior).

These results mean that we can accept that at a microclimatic scale there is a distinct pattern of variation in these environmental gradients which will affect the community of organisms that live within it. These effects are known to influence community structure, abundance, richness and diversity of organisms along a lateral gradient, so why not a vertical one?

Stratification of faunal communities (especially invertebrate) within the vertical structure can not only be determined by abiotic factors (such as those seen above), but also forest physiognomy and tree architecture, resource availability, and arthropod behaviour (Intachat and Holloway, 2000, Basset et al., 2003). Information regarding abiotic influences, resource availability and Diptera behaviour outside the context of the vertical column are available from a number of sources. For example we know that there are cases where temperature and humidity affect the emergence of certain families (Bishop et al., 1996), that plant phenology influence larval survival strategy (Boukili et al., 2007) and that increases of available habitat, favourable environmental conditions and food resources effect breeding behaviour (Kitching, 1972, Burtt et al., 1986, Schmidl et al., 2008). All these factors can be seen within the vertical gradient and are most apparent when we specifically look at the differences between dry and wet season results.

There are definite patterns in the abundance of Diptera within the canopy height classes and differences in those patterns between periods of rain and no rain. The driving forces behind these changes are important in understanding how the vertical stratification of dipteran abundance is affected by both height and seasonality. Overall dipteran abundance increased in periods of rain, however if we look at where the abundance increases we can see that abundance is stable in the ground canopy, whereas the abundance of Diptera increases significantly in the mid and high canopy during the rains. The suborder anf

group results (see fig 4.4 and 4.5) show that only the Nematocera have significant increases in abundance during the rains, and again these increases are located in the mid and high canopy strata. As Nematocera contribute to over 80 % of the overall abundance this explains the ordinal level data. In general Calyptrate, Acalyptrate and brachyceran abundances all reduced during the rain, although only the Calyptrates dropped significantly.

So why there is this shift in abundance in the Nematocera during periods of rain? To answer this we need to examine the ecology of the most abundant families. The results highlighted five families of Nematocera, of which the Cecidomyiidae were the most abundant. This family showed the most significant increase in abundance in the mid and high canopy strata during periods of rain (fig 4.6). However, the increase in abundance in this family is likely due to their life-cycle strategies than to specific environmental conditions. Although most studies on this family are related to crop protection, it is clear from the literature that the Cecidomyiidae are very vulnerable to changes in their habitat resulting from the phenology of their host plant as a majority of larvae from this family form leaf galls during their development. For example, when the host plant of *Rhopalomyia californica* is starting its growing season, it is more vulnerable to colonisation by the gall midge (Boukili et al., 2007) because physiological defence mechanisms are given less energetic priority than the production of new growth. The timing of elements of Cecidomyiidae life strategies are also tightly linked to their host plant and surrounding habitat. For example some species will overwinter in their leaf galls and then emerge directly from the gall, whereas others will drop to the ground, overwinter in the soil and emerge from the soil when climatic conditions are suitable (Tokuda et al., 2006). Therefore the results of this study suggest that there are diverse strategies among the Cecidomyiids in community within the Kwano forest which are linked to the strata they inhabit. The abundance in the ground canopy did not differ significantly between periods

of rain and no rain which suggests that these species are either ground emerging or that they are taking advantage of plants that grow leaves through the dry season (Chapman et al., 1999). However, the mid and high canopy species significantly increase in abundance during periods of rain. Studies such as Riberio (2007) and Paniagua et al. (2009) have suggested that the physiology of the leaf changes as height within the canopy increases, with factors such as leaf sclerophylly increasing while herbivory, fungal and parasitoid attack decrease. This proposed mechanism would have to be verified through further study. For example investigating the number of leaf galls within the canopy, discovering the exact triggers for emergence, and further taxonomic work that has not been possible within the scope of this project.

Life history traits of families such as the Chironomidae, which are mostly dependent on aquatic habitats for larval development, are understandably affected by rain within the ecosystem. Periods of rain not only increase the available larval habitat, but the increased humidity would also increase the amount of microbial activity in the leaf layer, increasing the breakdown of organic matter and therefore increasing the availability of feeding resources for the Chironomidae larvae (Liu et al., 2005). There was no overall significant difference in abundance of Chironomidae between heights within periods of rain or no rain; however there was a significant increase in abundance in the mid and high canopy once the rains had started. The ground canopy abundances were probably highly influenced by a single emergence event during the rains of 2010, when 156 chironomids were captured in a single trap over a 24 hr period. This was well above the average (~ 4) for this period and at this height. Repeat Mann-Whitney analysis, once this outlier is removed, shows that there is in fact a significant difference between the ground and high canopy Chironomidae abundances, $z = -2.654$, $p < 0.01$, but no significant difference between seasons in the ground canopy, $U = 635$, $z = -1.56$, *ns*. This is again following the

same pattern at the other Nematocera, with no overall increase in abundance in the ground canopy but significant increases in the upper layers of the canopy.

Availability of larval development habitat does not however restrict the adult Chironomidae to aquatic habitats. It is reasonable to suggest that other factors such as the availability of feeding resources or favourable environmental conditions are more likely to determine where the majority of the adult abundance is found within the canopy. Adult Chironomidae feeding behaviour was once thought to involve no food intake whatsoever (Miall and Hammond, 1900); however later investigation has found that the adults of most species do feed on materials containing sucrose and glucose (Burtt et al., 1986). These materials can take the form of nectar or honeydew, which would have a much higher presence in the canopy during periods of rain, as tree species in the tropics increase their flowering at the start of the rains (Bawa et al., 2003), and could therefore go some way to explaining the greater abundance of chironomids in the canopy during this period. Burtt et al. (1986) showed that male and female Chironomidae use the energy gained from both feeding and from stores prior to emergence in differing ways; with males increasing their flight time by 160 % but not their longevity and females not increasing their flight time but increasing their longevity by 40 %, however the authors believed that the females emerge with greater reserves of energy than the males as even when starved they have a significantly greater longevity than males. The authors attributed this to possible mating behaviour, with males trying to increase the number of females they could encounter and females optimising the time in which to successfully deposit eggs. This may account for the increased swarming behaviour within the canopy with males optimising their breeding strategy when food resources are at their highest. Increased rain fall would also provide larval habitat within the canopy itself, by filling available tree holes with rain water, which is a well known chironomid larval habitat (Kitching, 1972, Schmidl et al., 2008). These

are both life history traits that are intertwined with the coming of the rains but not necessarily a consequence of changes to the microclimate within the canopy.

The Ceratopogonidae show a similar pattern to the Cecidomyiidae and Chironomidae, in that the abundance in the mid and high canopy categories increases during periods of rain. Ceratopogonidae are blood suckers, who prey on vertebrates ranging from mammals (they are a vector for Bluetongue disease, see Nolan et al. (2008)), birds and reptiles. Several sources of literature have studied the emergence behaviour of this family and some have found that temperature plays an important role in the timing. Studies in Australia found that there is a temperature band of 17 to 36 ºC in which the greatest number of individuals emerge; with males dominating the lower temperatures within this range and female emergence dominating higher temperatures (Bishop et al., 1996). In Kwano during no rain periods the minimum and maximum temperatures can fall well outside of this band (see sections 4.3.1). Therefore with the narrowing of the temperature window during rain periods it becomes the perfect environmental conditions for the emergence of the Ceratopogonidae. Available habitat for emergence also increases during periods of rain as many Ceratopogonidae species prefer soil/mud/dung that is adjacent to freshwater in which to lay their eggs (Uslu and Dik, 2010). However these ecological factors only explain the greater abundance of this family during periods of rain, it does not explain the differences in abundance through the vertical column.

The results show that the abundance of ceratopogonids did not significantly change in the ground canopy; it was only the mid and high canopy abundances that significantly increased once the rains had started. Vertical stratification in Ceratopogonidae has been shown before (although over smaller differences in height and in temperate forest) and this was attributed to host specialisation (Swanson and Adler, 2010). Ceratopogonidae will feed on a variety of vertebrate species including birds. Avian breeding seasons in the

tropics tend to coincide with the wet season (see Jahn et al (2010) for example), therefore with increased avian breeding during periods of rain there is an increase in potential prey items for the Ceratopogonidae. Swanson and Adler (2010) showed that in temperate forests the community of Ceratopogonidae varied, even over a small height increase of 0 to 10 m, dependent on their host associations, with mammalophilic species tending to be captured closer to the ground and avianophilic species being captured higher in the canopy.

Whereas the three most abundant families of Nematocera showed no significant difference attributable to rainfall in their respective ground canopy abundances, the Calyptrates did respond to rain. Both richness and abundance of the four most abundant Calyptrate families fell significantly during periods of rain (figs 4.7 – 4.10). There were significant reductions in abundance of Tachinidae and Muscidae in the ground canopy during periods of rain, and Sarcophagidae and Calliphoridae showed a much higher preference for the high canopy during dry periods but this was again reduced during rain. Mid and high canopy Tachinidae were the only populations to maintain their abundance during periods of rain. The four Calyptrate families investigated here are mostly associated with dung and carrion (Stubbs and Chandler, 1978), which would be just as prevalent during the rains as it was in the dry periods. However there is the question of competition with other orders of invertebrate. For example, dung beetles, Scarabaeoidea, have a much higher abundance in the wet season (Hernandez and Vaz-de-Mello, 2009), and could provide significant competition to dung and carrion feeding Diptera. With the exception of the arboreal *Canthonini* dung beetles, most dung beetles prefer the forest floor as there is a lack of large vertebrate species producing dung within the canopy (Jacobs et al., 2008); therefore it would make sense for the dung and carrion feeding flies to either move to the higher canopy or simply overwinter as larval forms during periods of rain.

What is clear is that the change in the seasons has a very profound effect on not only the overall abundance of Diptera, but also on where they are found within the vertical column. The suggested reasons for why these changes in vertical stratification occur, given in this chapter, require further investigation in the future. For some species, such as those in the Ceratopogoniodae, temperature may indeed play an important role in determining emergence, but without the rain this would not happen. Niche speciality is a significant factor in determining the vertical stratification of the families studied, whether through a specific mating or feeding strategy, or through the avoidance of competition with other taxa.

Chapter 5: The effect of burning adjacent savannah on dipteran communities within the forest edge

5.1 Introduction

In Chapter 1 the practice of savannah burning was discussed. That section showed that this anthropogenic management practice has been used for many thousands of years, and that it is only since colonialism that its ecological benefits have been questioned. What was clear from the literature was that there was distinction between early season burning and late season burning, with early season burning being more favourable than late (Bucini and Lambin, 2002).

Late burning was observed within the Kwano forest during the research period (although not at the sites studied here), and its effect on the edge of the forest was quite profound. From personal observations the fire spread much further into the forest boundary during late dry season than in early dry season, causing damage to the understory (ground canopy) and removing small trees, shrubs and saplings, and causing damage to the lower branches of the trees. Early dry season fires did not seem to enter into the forest boundary and only maintained the boundary between savannah and forest. This may be the result of possible higher moisture content in the vegetation and ground litter preventing the spread of fire (Bucini and Lambin, 2002). There may also be an element of anthropogenic management, ensuring that the fire will not spread into the forest either by careful observation of the prevailing winds or by the use of fire breaks dug adjacent to the forest boundary.

Although burning savannah is technically illegal within Nigerian National Parks, the practice still continues within the Gashaka Gumti park boundary, even far away from the village enclave of Gashaka itself, where burning of agricultural plantations is generally accepted by the park management. The Kwano field station lies just off an ancient

footpath that connects the villages of Gashaka and Selbe, roughly two hours walk from Gashaka and four from Selbe. As this footpath is regularly traversed by the indigenous human population the opportunity to set fires at the path edges is apparent, and easily observed during the dry season.

When speaking to the local inhabitants as to why they believe that the savannah should be burnt, most will say that it is because it increases new growth in the grass and therefore encourages large herbivorous mammals into the area. However, as the grazing of domesticated livestock and hunting of wild animals is strictly forbidden and enforced, this reason seems to hold little water in the context of the National Park. From the literature (such as Laris (2006)) we can also see that the early burning of savannah is also used as a preventative measure against late season accidental or wild fire, which would cause damage to adjacent forest in the latter part of the dry season.

This study is looking specifically at the effect of burning at the forest edge on the population of Diptera. Such studies have not been carried out before so this is the first real opportunity to detect any changes in abundance or community structure that the burning might cause. In the ordinal results (Chapter 3) we saw that there was no significant differences in the total abundance of Diptera between burnt and non burnt edges of the forest (< 100 m from the savannah forest interface), but as we saw with the vertical stratification, once the total abundance data is broken down into sub order or family level data, trends and significant differences emerged.

In this chapter, savannah data collected during the pilot phase of the study will also be analysed in greater detail. Again in the ordinal results (Chapter 3) we saw that burning had no overall effect on the total abundance of Diptera within the savannah. However there were positive effects of burning found in the wet season, with non burnt edges showing a

decrease in abundance during the rains. The abundance of Diptera in the forest increased during periods of rain, so for the non burnt savannah matrix to have a reduced abundance is a situation that deserves further investigation. The previous chapter also showed that Nematocera are the most important sub order of Diptera in terms of total abundance and explained a majority of the variation in vertical stratification, so the effect of burning on these families also needs to be investigated.

5.2 Methodology

The sample collection followed the protocols described in Chapter 2, but the data analyses will focus on how the burning savannah affects the population of Diptera within the forest boundary and in the savannah itself.

Is was necessary to makes sure that the two savannah areas adjacent to forest plots were similar in dipteran community structure so that changes in community after burning could be attributed to the process of burning and not to a pre-existing difference. Therefore the samples taken from the savannah pre and post burning, and from the non burnt savannah in both wet and dry seasons were analysed.

In order to understand the differences between the two treatment edges, it was first necessary to confirm that it was the burning of the adjacent savannah causing any differences found and not because the forest edges were different in terms of vegetation structure and complexity. To do this the distance to nearest vegetation data were used to asses the structural similarities and vegetative densities. Possible differences in environmental conditions were also assessed, as Chapter 4 showed how significantly some

of the studied dipteran families are affected by seasonality, there also might be an effect of changes in humidity and temperature.

Statistical analysis was performed through parametric and non parametric ANOVA, with appropriate post hoc analysis were necessary (see Chapter 3 and 4 for more detailed statistical methodology). In Chapter 4 the 'z' statistic was reported for Mann-Whitney post hoc analysis, however in this chapter sample size is sometimes less than this therefore the '*U*' is reported instead. In addition to the parametric and non parametric ANOVA analysis, CCA analysis was also conducted. Using CANOCO for Windows environmental and structural factors were used to assess the distribution of dipteran families.

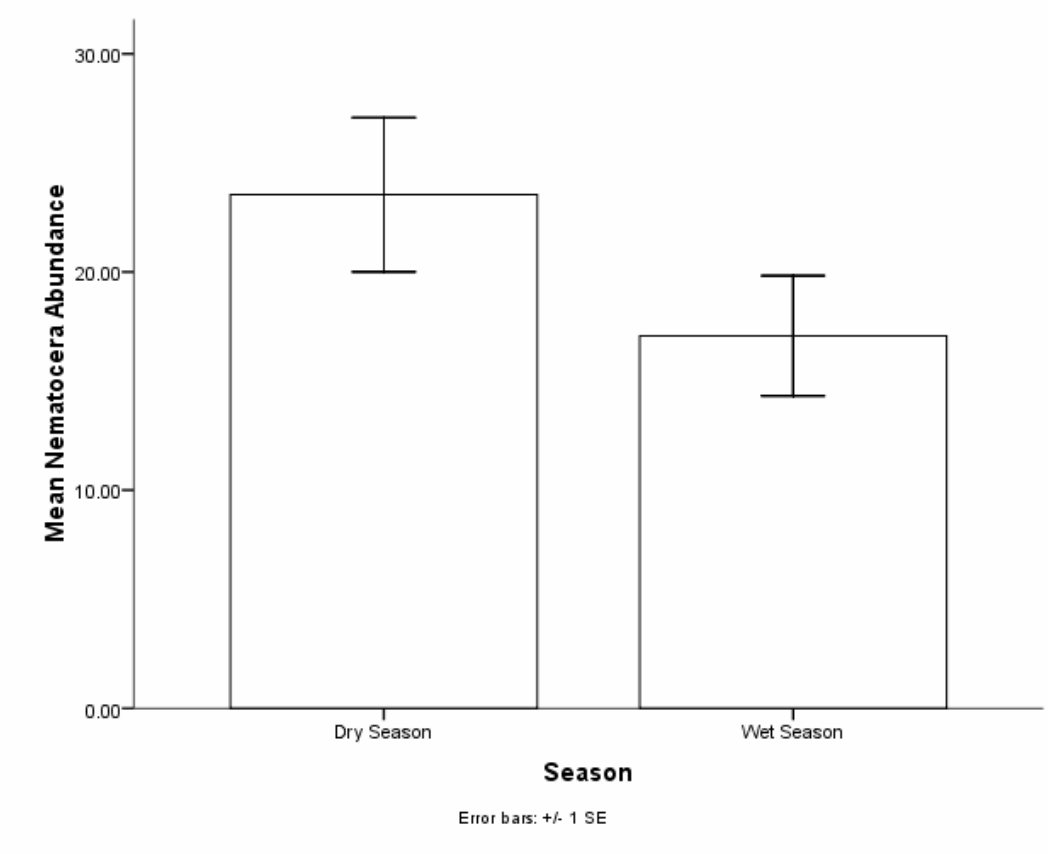
5.3 Results

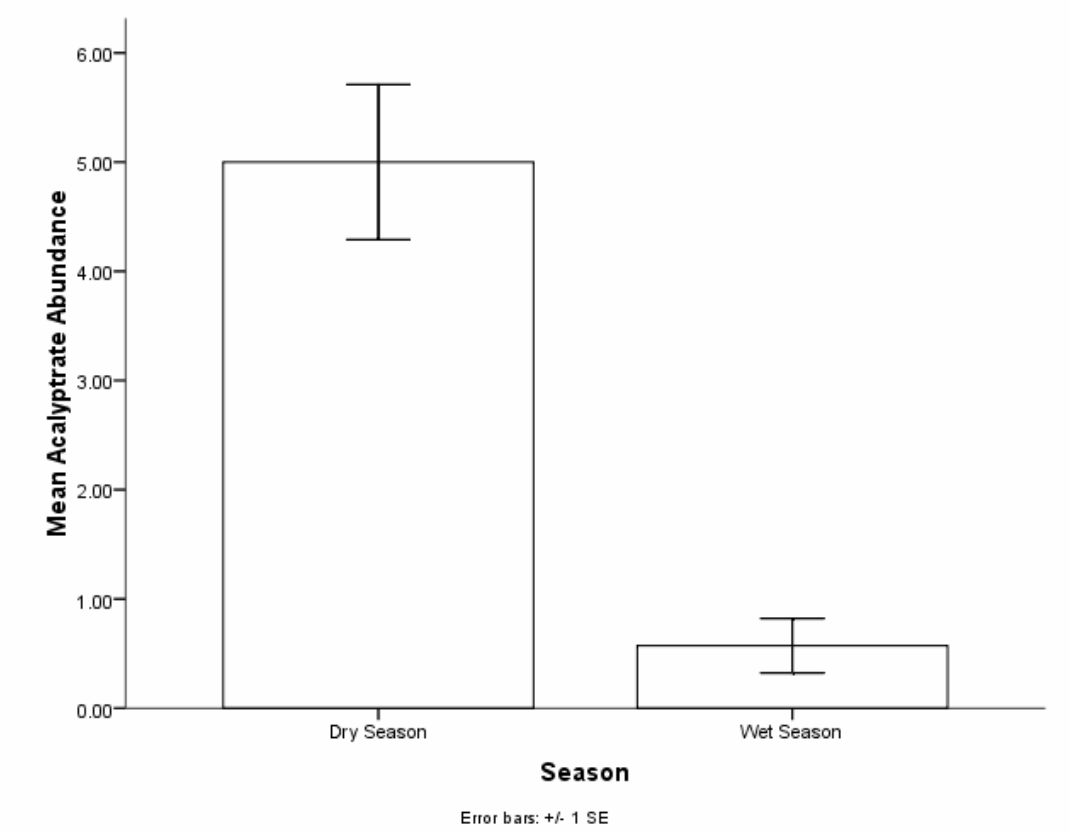
5.3.1 Effects of burning on savannah Diptera abundance

A total of 1192 Diptera were captured in 38 samples during the savannah pilot phase of this project (mean = 31.4, *sd* = 19.3 per trap day). Within these samples Nematocera represented 67.4%, Calyptrate 17.8%, Acalyptrate 10.5% and Brachycera 4.3 % of total abundance. The effects of savannah burning on total Diptera abundance was described in an earlier chapter (see Chapter 3), so here sub order and family level data will be analysed. As Brachycera represented only a small percentage of abundance they were discounted for this analysis. The remaining sub orders had a normal distribution, so ANOVA was used to analyse how treatment and season affected their abundance.

A one way ANOVA was used to test for differences between seasons within the three sub orders. Nematocera showed no significant difference between seasons, F (1, 37) = 1.61, *ns*,

however Acalyptrates and Calyptrates showed significantly higher abundance in the dry season, F (1, 37) = 21.57 $p < 0.001$ and F (1, 37) = 26.75, $p < 0.001$ respectively (see figure 5.1 below).





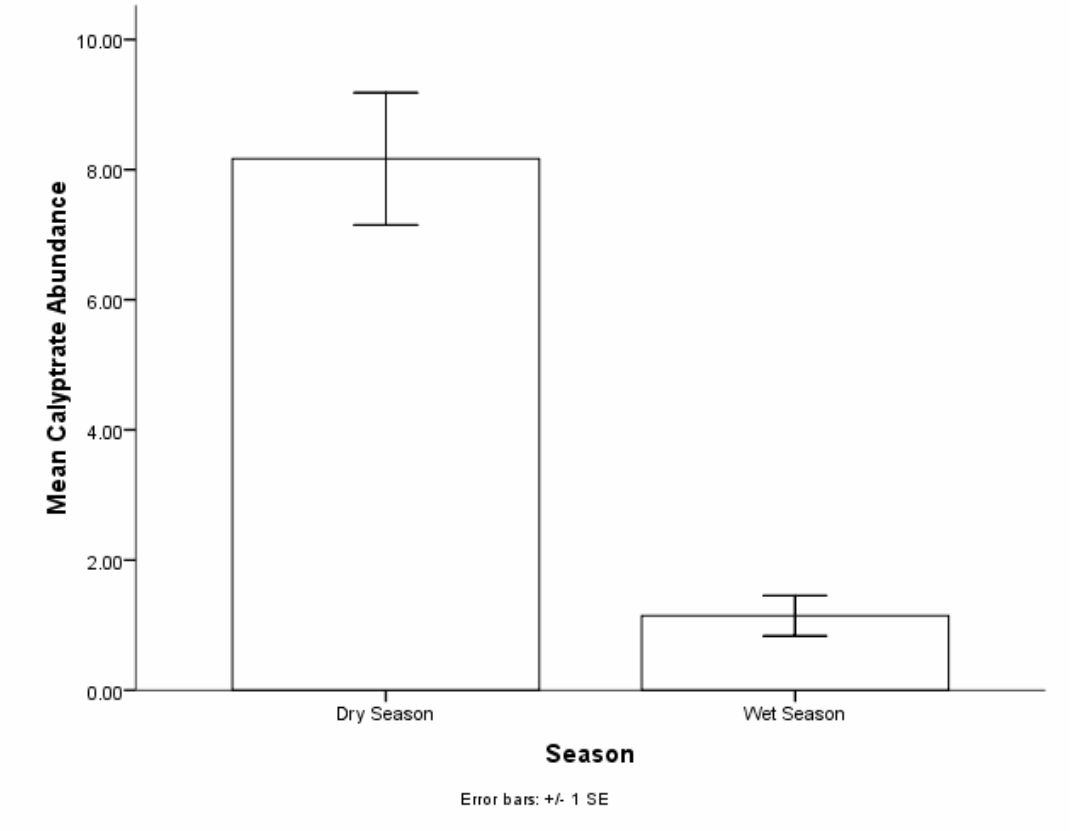
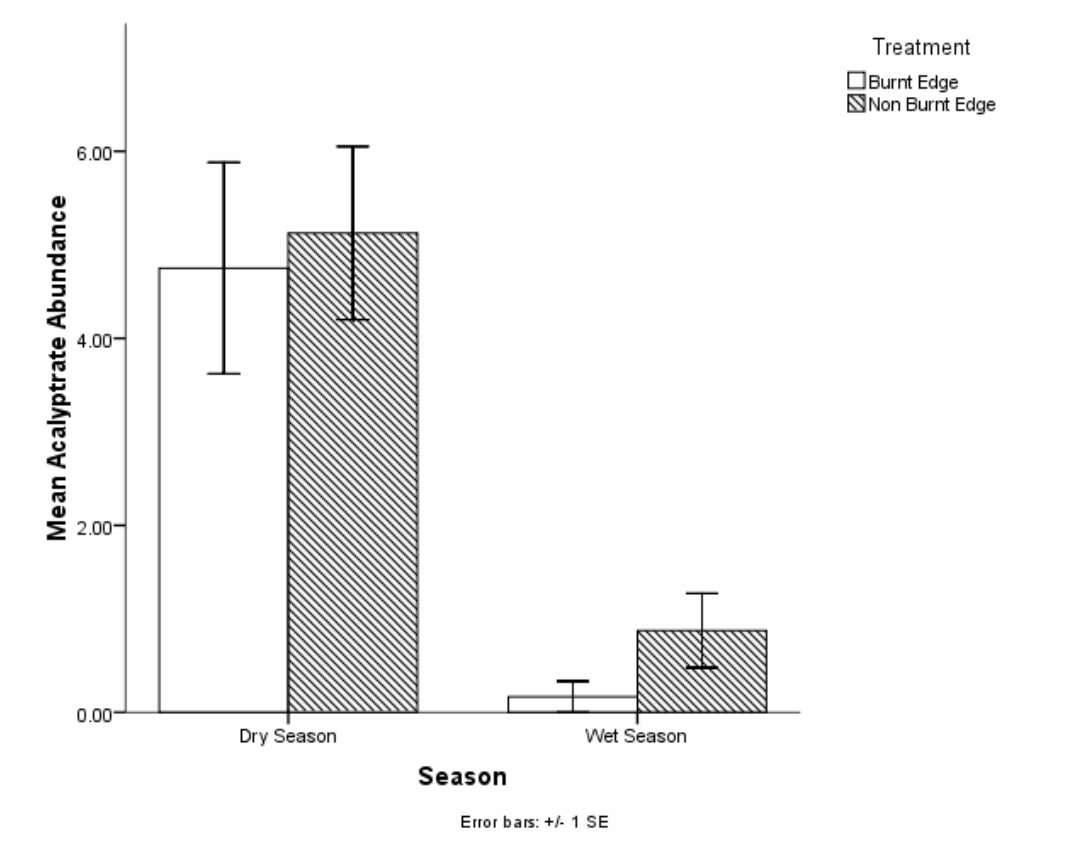


Fig 5.1 Differences in abundances (per trap day) of three sub orders of Diptera in adjacent Kwano savannah.

A two-way ANOVA was used to test for significant differences in the abundance of the three sub orders with season and treatment (burnt or non burnt savannah) as factors. The

corrected model for the Nematocera proved not to be significant, F (1, 37) = 0.57, *ns*, with neither of the factors having a significant influence on the abundance. Acalyptrate, F (3, 37) = 6.95, $p < 0.005$, and Calyptrate, F (3, 37) = 11.54, $p < 0.001$, both showed a significant component to the corrected model; however in both cases season was the overriding significant factor, F (1, 37) = 19.29, $p < 0.001$ (Acalyptrate), and F (1, 37) = 32.91, $p < 0.001$ (Calyptrate), which has already been shown. Figure 5.2 illustrates these differences.



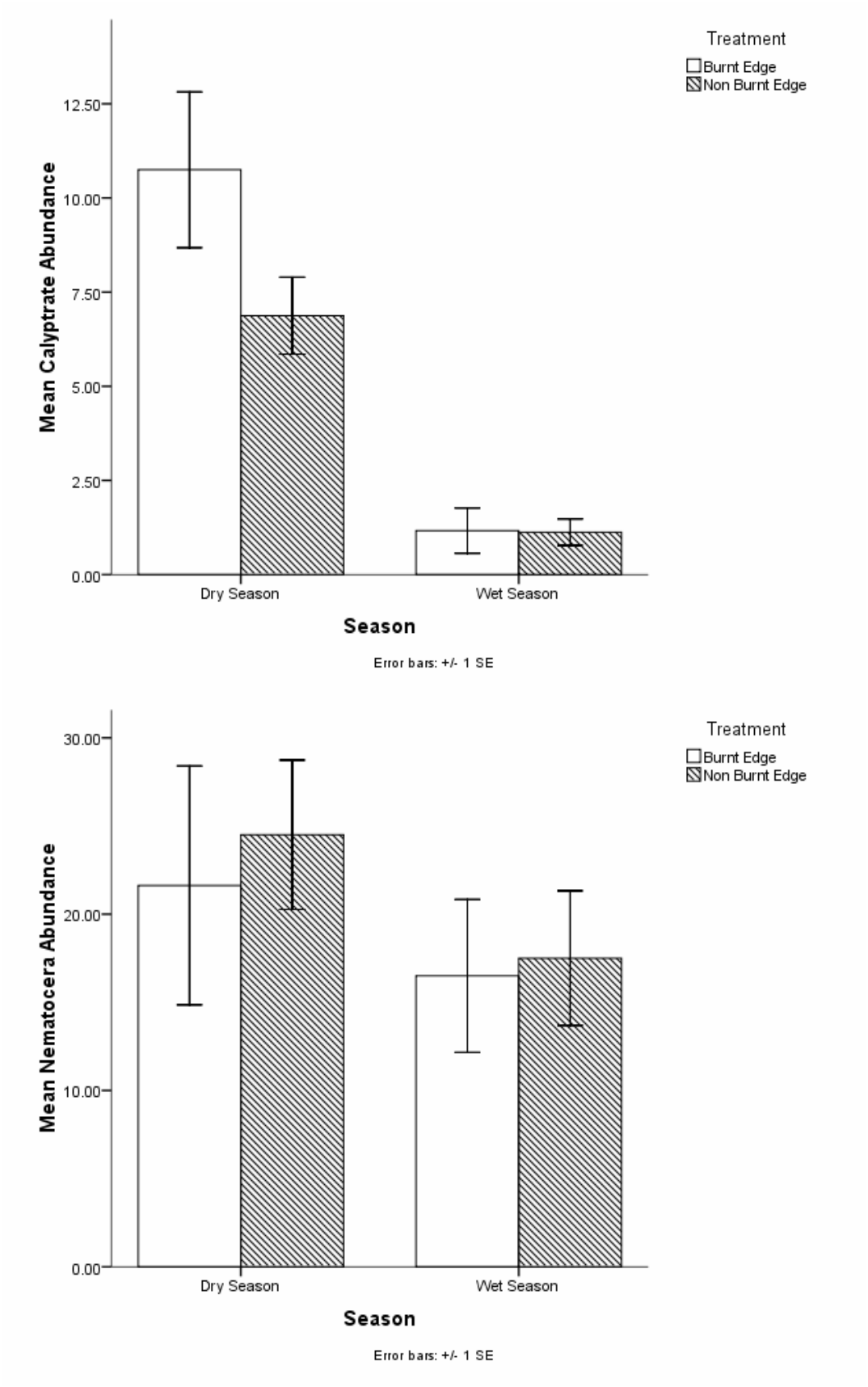
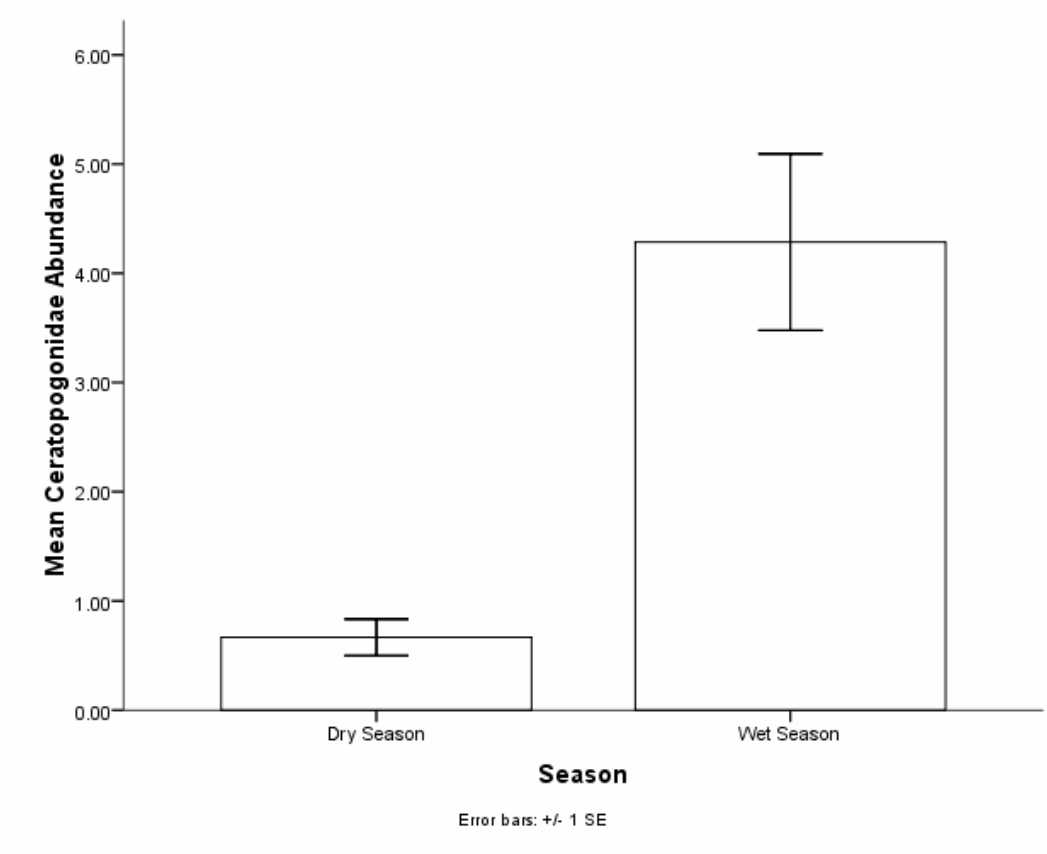
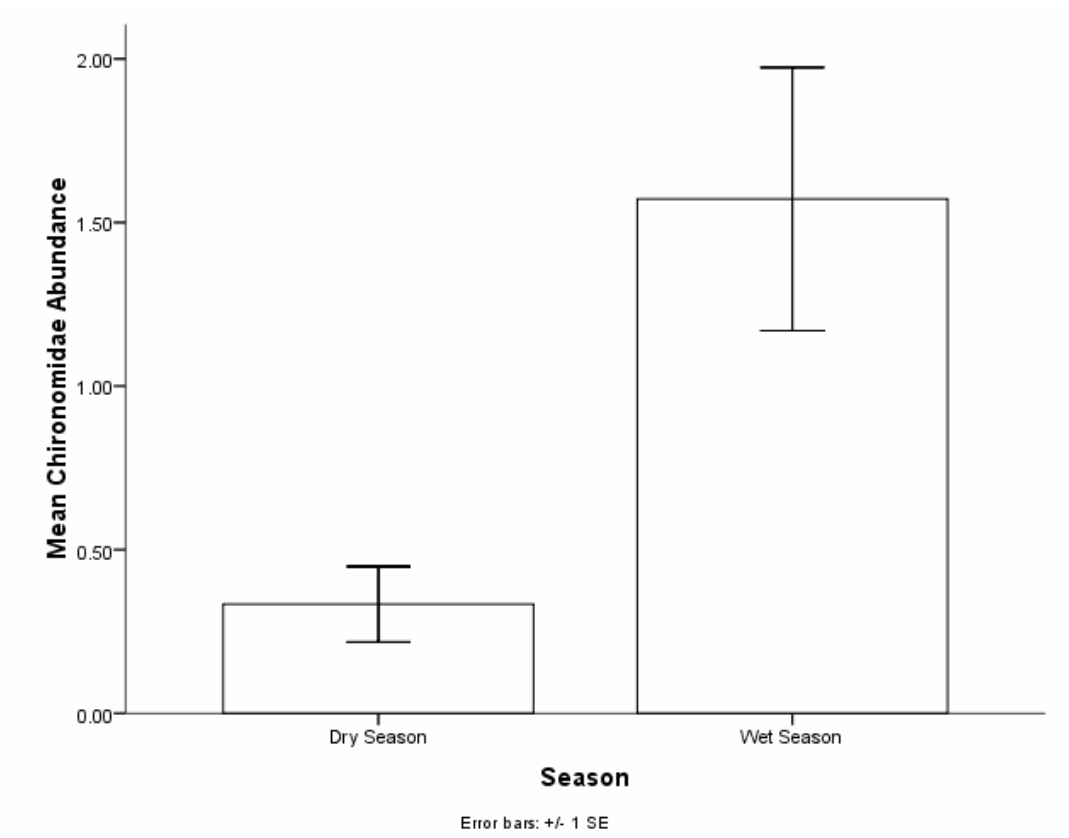


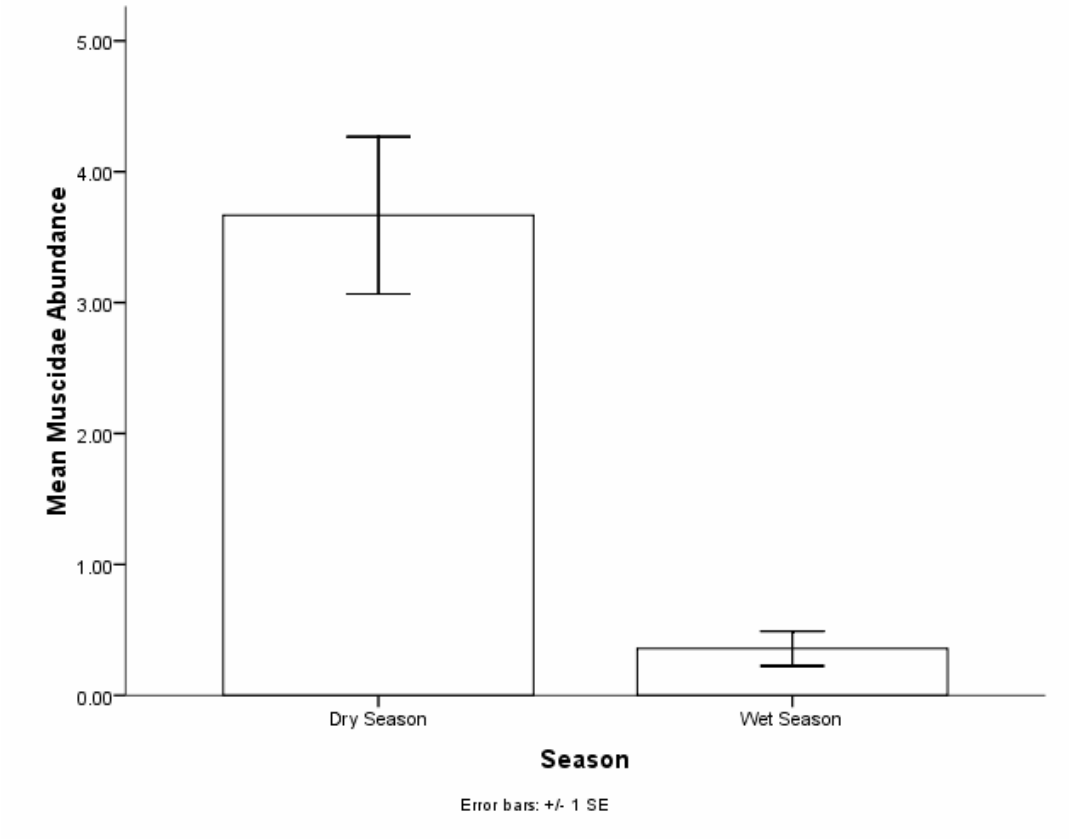
Fig 5.2 The effects of season and treatment on the abundance (per trap day) of Nematocera, Calyptrate and Acalyptrate, Kwano savannah.

From the above graphs we can see that although there is no significant difference, there is a definite trend in the data, with the Calyptrate strongly associated with the burnt edges during the dry season. Four families have been chosen from these sub orders for further analysis, these are; Ceratopogonidae, Cecidomyiidae, Chironomidae and Muscidae, representing blood suckers, gall forming, aquatic associated and dung/carrion associated species respectively.

A one-way ANOVA showed that the Cecidomyiidae, F (1, 37) = 11.00, $p < 0.001$, and Muscidae, F (1, 37) = 17.213, $p < 0.001$, both significantly decrease in abundance during the wet season. By contrast Ceratopogonidae, F (1, 37) = 31.07, $p < 0.001$, and Chironomidae, F (1, 37) = 13.27, $p < 0.005$, both increase in abundance during the wet season (see fig 5.3, below).




Mean Chironomidae Abundance
2.00
1.50
1.00
0.50
0.00
Dry Season
Wet Season
Season
Error bars: +/- 1 SE


Mean Muscidae Abundance
5.00
4.00
3.00
2.00
1.00
0.00
Dry Season
Wet Season
Season
Error bars: +/- 1 SE

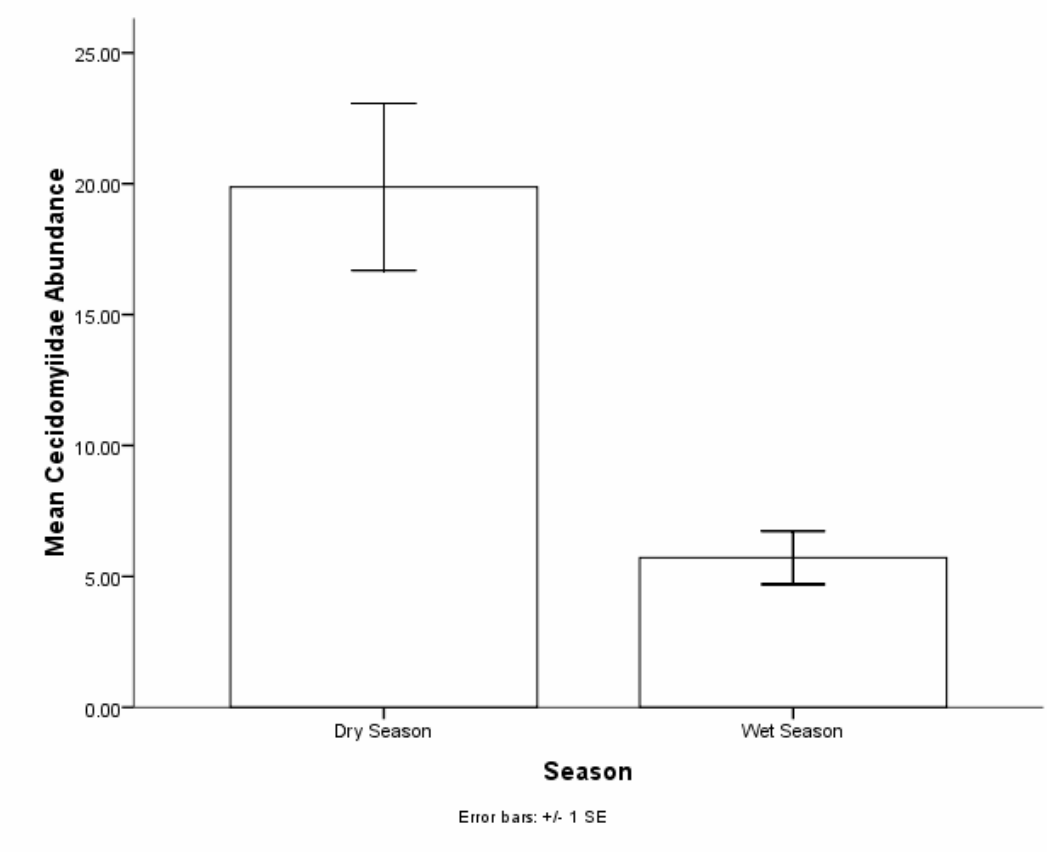
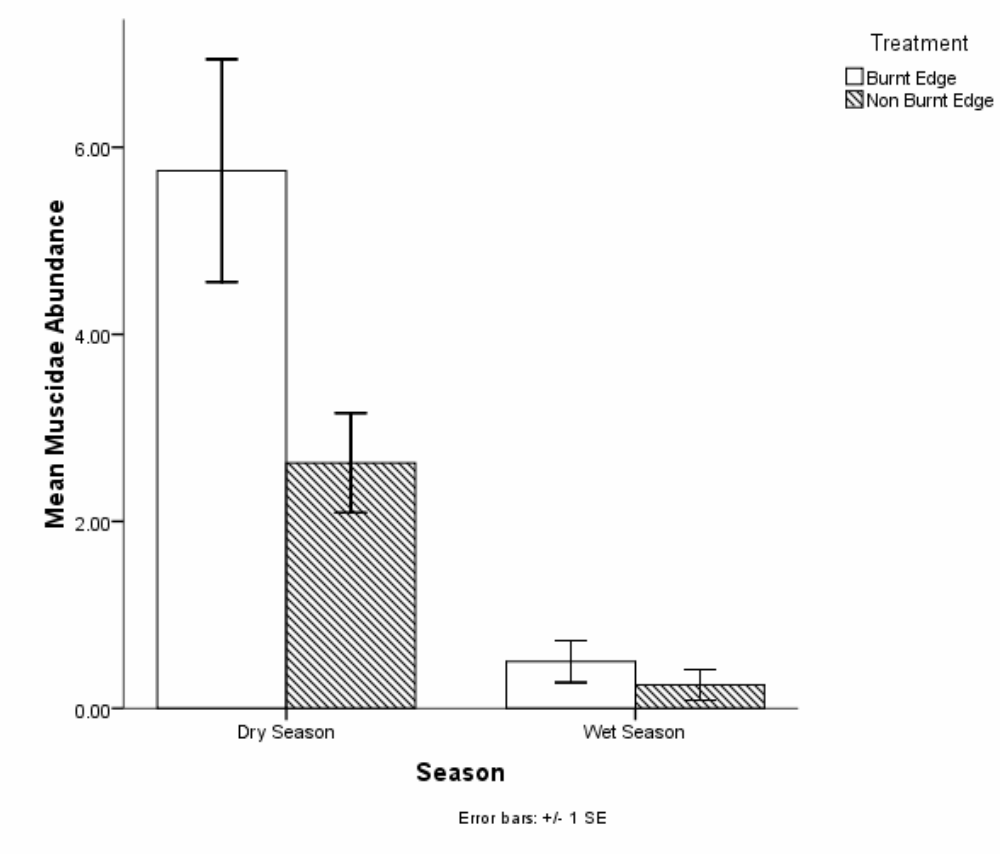


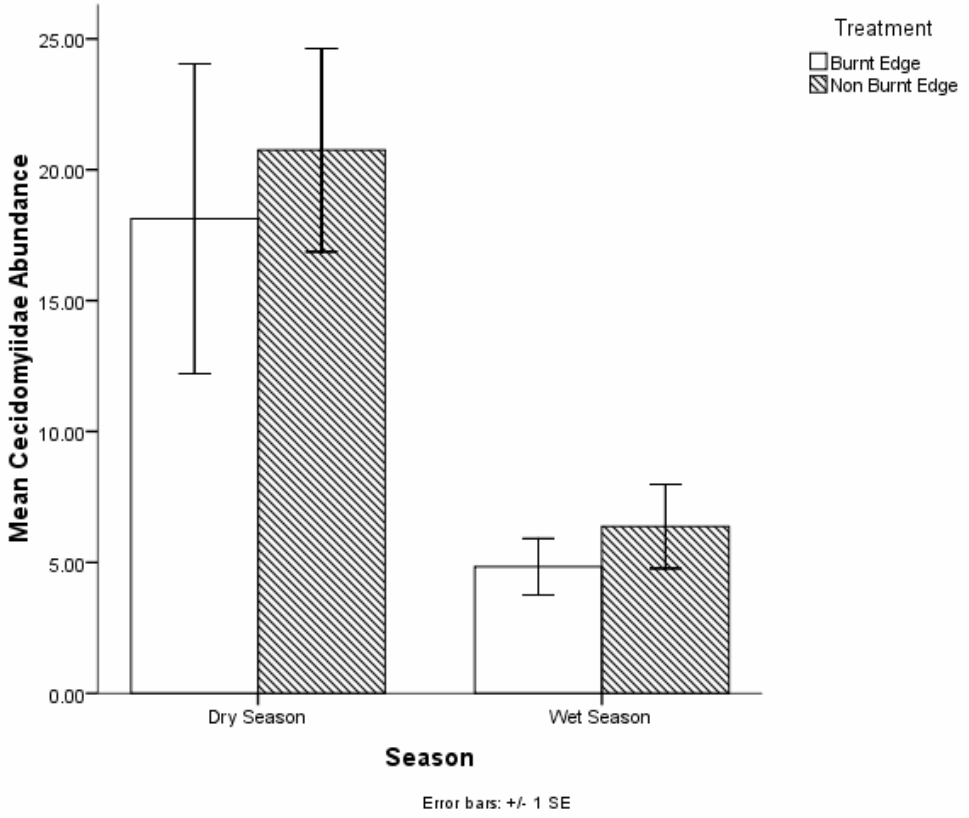
Fig 5.3 Differences in seasonal abundance (per trap ay) in four families of Nematocera, Kwano savannah.

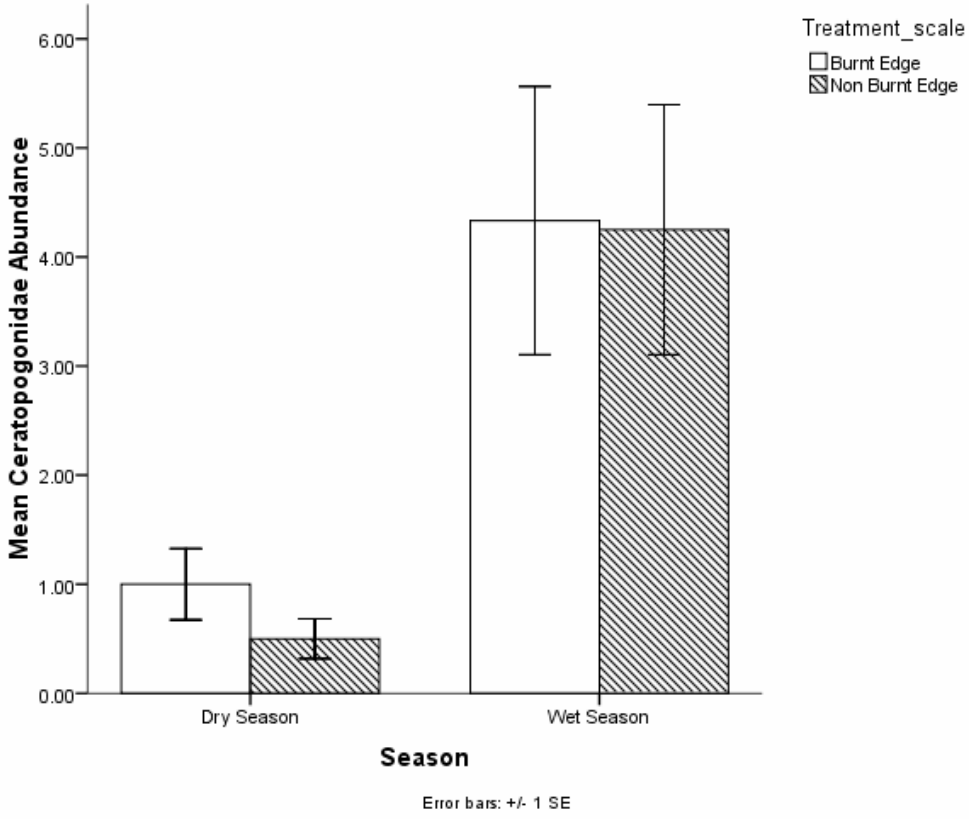
The two-way ANOVA used to test for the effect of treatment and season showed that the Nemotocera families Ceratopogonidae, Chironomidae and Cecidomyiidae all had significant components within the corrected model. However as with the sub order analysis these significant differences all came from the seasonal effects rather than the burning treatment. However unlike the sub order and Nemotocera analysis the Muscidae showed significance within the corrected model, where there was a significant difference in both the seasonal abundance, F (1, 37) = 27.46, $p < 0.001$, and in the abundances between treatments, F (1, 37) = 5.38, $p < 0.05$.

To further explore the differences in abundances under different treatments, the data were split by season and the treatments compared using a Mann-Whitney test. The results showed that there was a significantly higher Muscidae abundance in burnt savannah during the dry season (immediately after burn), $U = 27$, $p < 0.025$ (Bonferroni corrected),

however there was no significant difference in abundance during the wet season, $U = 18$, *ns*. Figure 5.4, below shows these differences.




Treatment
Burnt Edge
Non Burnt Edge
Mean Cecidomyiidae Abundance
25.00
20.00
15.00
10.00
5.00
0.00
Dry Season
Wet Season
Season
Error bars: +/- 1 SE


Treatment_scale
Burnt Edge
Non Burnt Edge
Mean Ceratopogonidae Abundance
6.00
5.00
4.00
3.00
2.00
1.00
0.00
Dry Season
Wet Season
Season
Error bars: +/- 1 SE

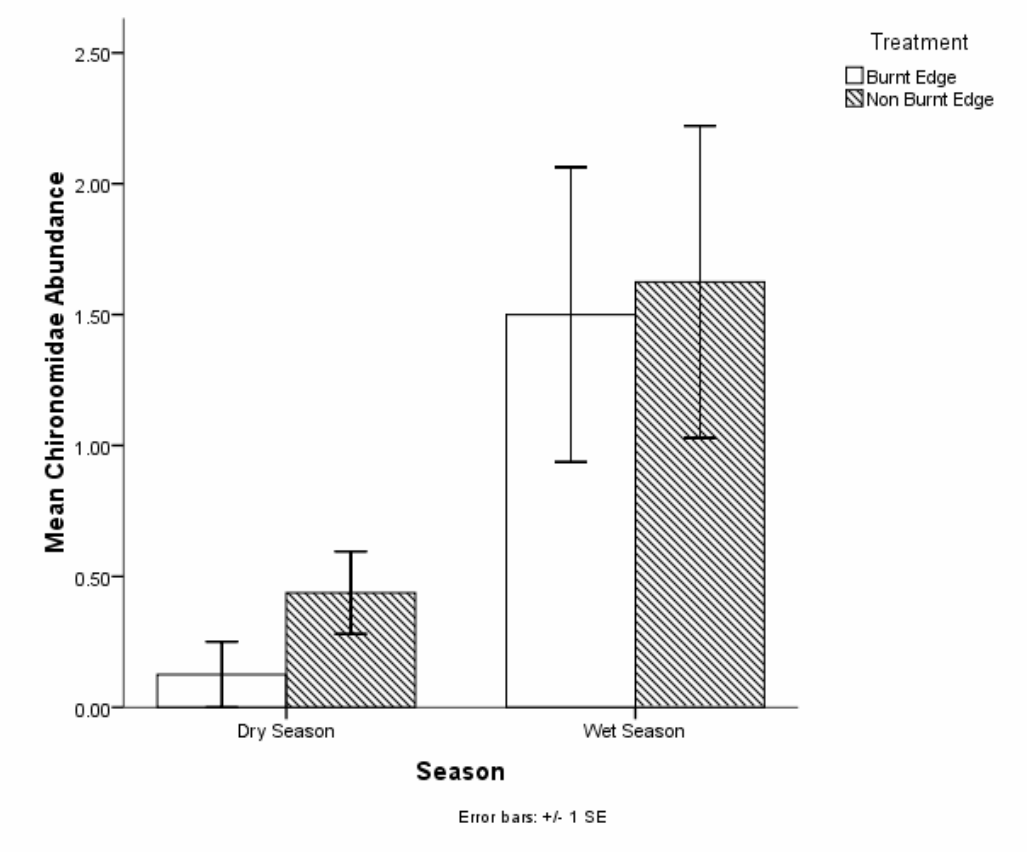
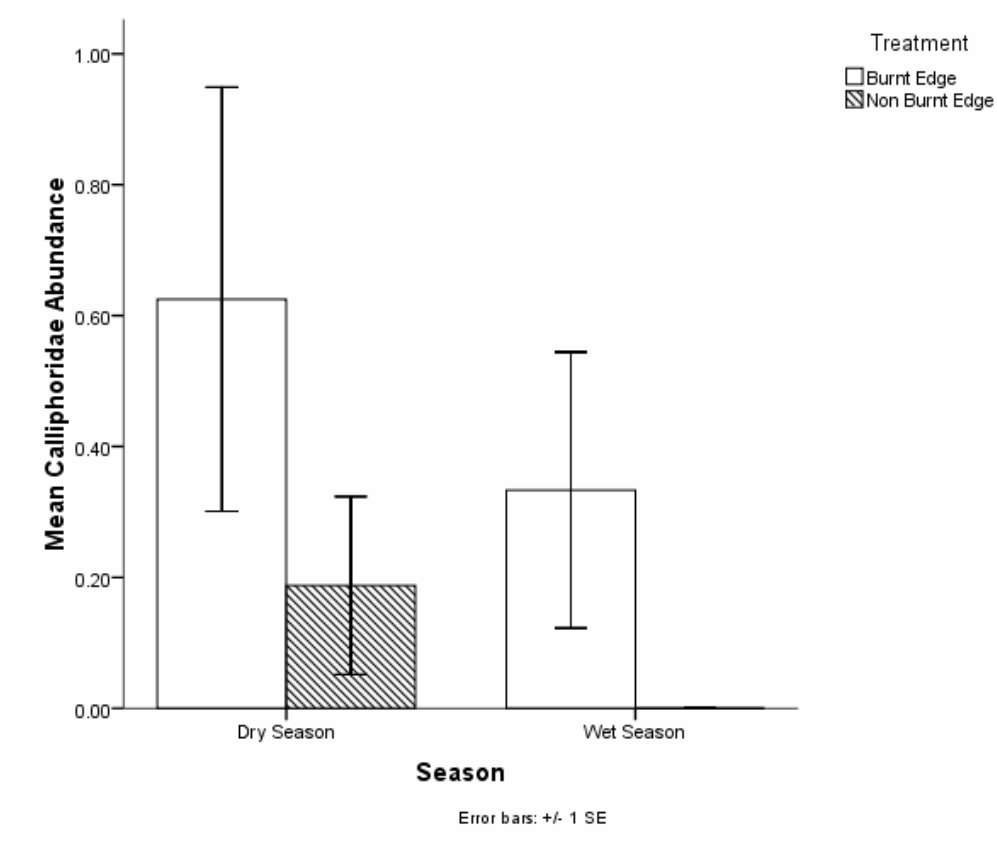


Fig 5.4. Differences in dipteran abundance (per trap day) between treatments and season in four Nematocera families, Kwano savannah.

As the Muscidae had such a clear reaction to the burning of the savannah, other Calyptrates were also analysed to look for similar traits. As in the previous chapter Tachinidae, Sarcophagidae and Calliphoridae were included, however due to the non normal distribution of data, small sample size and relatively low abundance non parametric analysis was used.

Previous analysis has shown that Calyptrate abundance fell dramatically during the wet season so no further analysis was needed here, therefore these three families were simply analysed using a Mann-Whitney test on data split between seasons. None of the three families showed any significant difference between burnt and non burnt abundances, yet there is a definite trend in the Sarcophagidae, $U = 48.5$, $z = -1.04$, *ns*, and Calliphoridae, $U = 47.5$, $z = -1.43$, *ns*, following that of the Muscidae, and the results here may just be a case

of sample sizes being to small to analyse accurately. Figure 5.5, below, illustrates these trends.



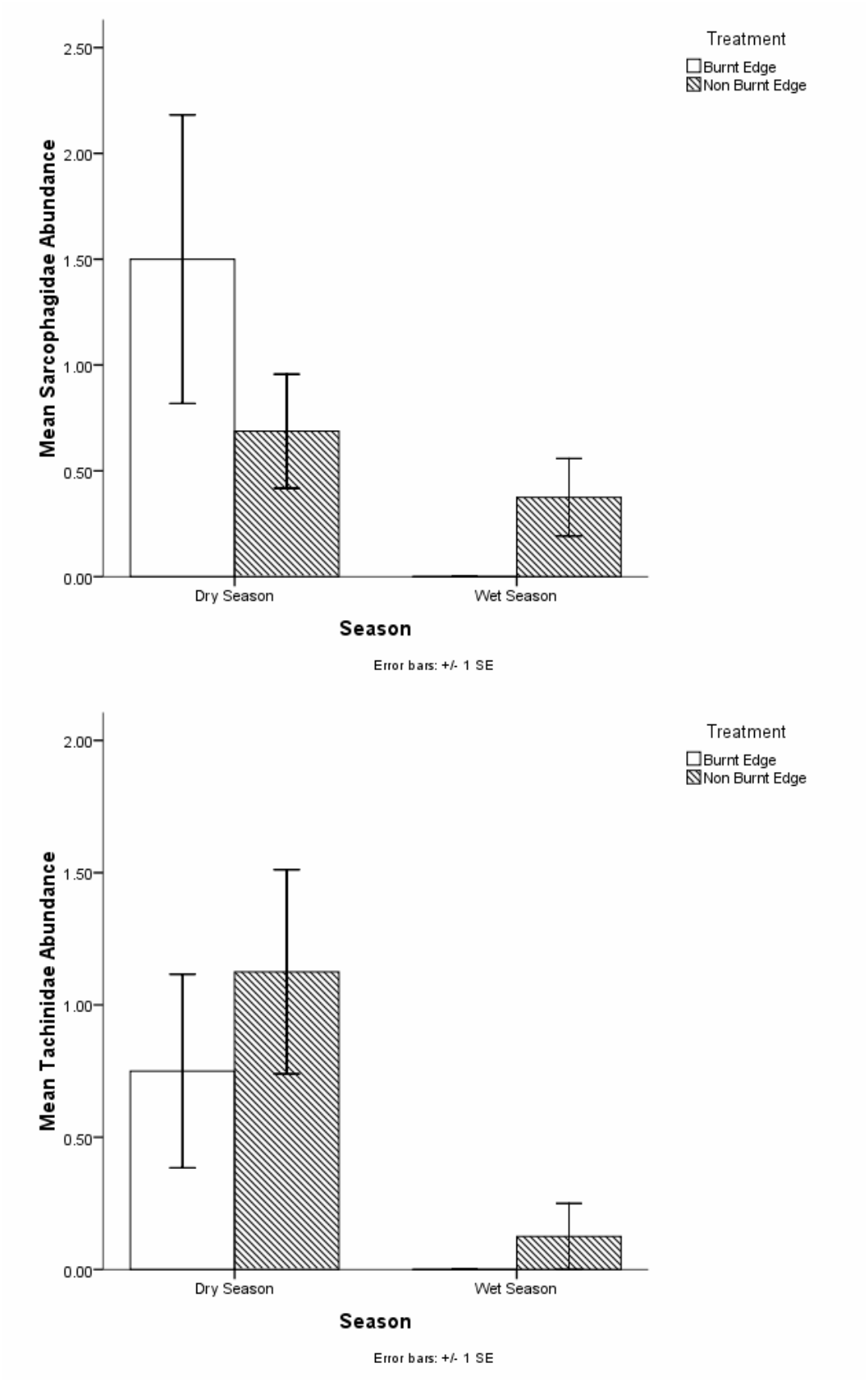


Fig 5.5. Differences in abundance (per trap day) of three Calyptrate families between burnt and non burnt treatments, Kwano savannah.

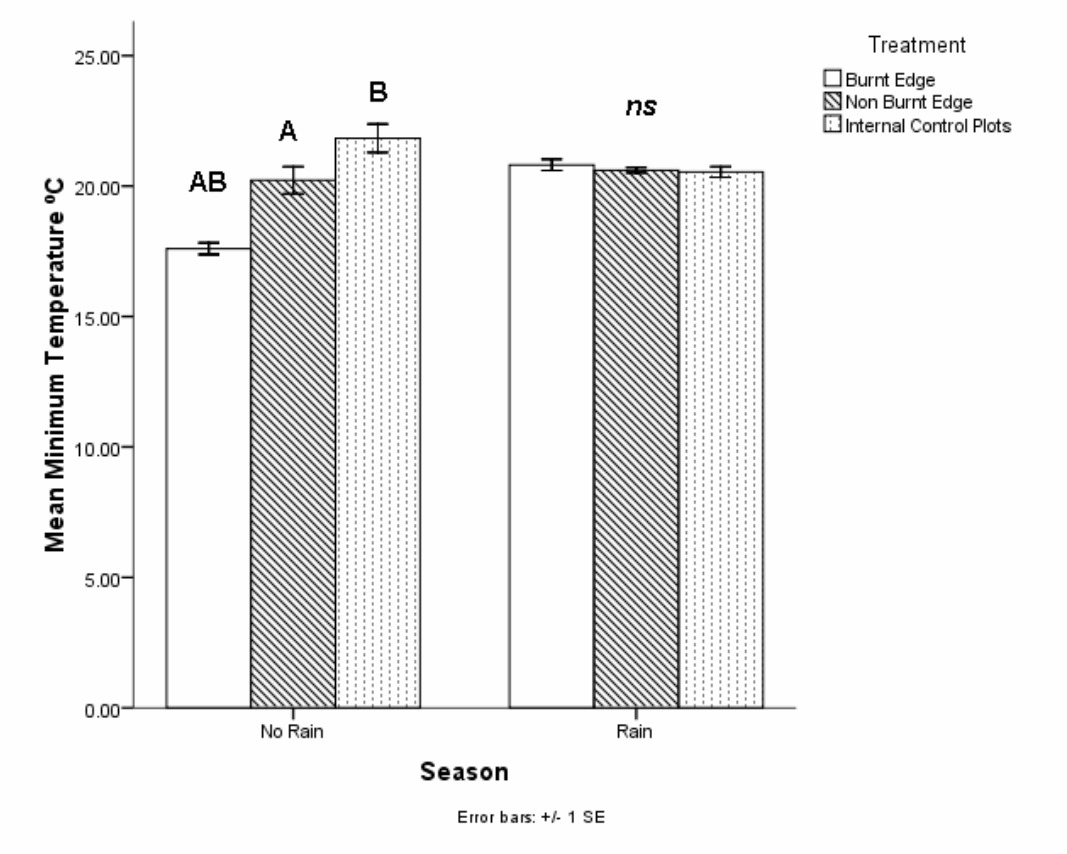
5.3.2 Environmental and habitat changes at the forest edge due to burning of adjacent savannah

The previous section has shown that there is a trend in abundance for some families of Diptera towards either one of the edge types or towards the internal areas of the forest. Here the environmental differences in these areas will be taken into account.

Environmental variables were checked for normal distribution and with the exception of maximum humidity were found to be normal (by a one-sample Kolmogorov-Smirnov test). As in previous environmental analysis the reason for the maximum humidity being non normally distributed is due to it generally being 100 % RH during periods of rain. Therefore for this analysis it has been discounted. However, minimum humidity, and maximum and minimum temperature will all be used in this analysis.

Initially the environmental parameters were analysed with a one-way ANOVA between treatments within periods of rain and no rain. In the dry periods minimum temperature, F (2, 43) = 20.641, $p < 0.001$, maximum temperature, F (2, 43) = 4.622, $p < 0.05$, and minimum humidity, F (2, 43) = 25.099, $p < 0.001$, all showed significant effects of burning treatment (see fig. 5.6). Tukey post hoc analysis showed that the minimum temperature was significantly lower at the burnt edge than both the non burnt edge, $p < 0.001$, and internal control plot, $p < 0.001$. Maximum temperature was significantly higher in the non burnt plots than in the internal control plots, $p < 0.05$, and the minimum humidity was significantly lower in the burnt edge than in the non burnt edge, $p < 0.005$, and the internal control plots, $p < 0.001$, and the non burnt plots were significantly less than the internal control plots, $p < 0.005$.

During the rains minimum temperature showed no significant differences between treatments, F (2, 82) = 0.469, *ns*, whereas both maximum temperature, F (2, 82) = 3.762, $p < 0.05$, and minimum humidity, F (2, 82) = 5.729, $p < 0.005$, showed significance between groups. Tukey post hoc analysis showed that the maximum temperature was significantly higher in the internal control plots than the non burnt edge, $p < 0.05$, and the minimum humidity was significantly lower in the internal control plots than in both the burnt, $p < 0.05$, and non burnt, $p < 0.05$, edge plots. Figure 5.6, below, illustrates these difference.



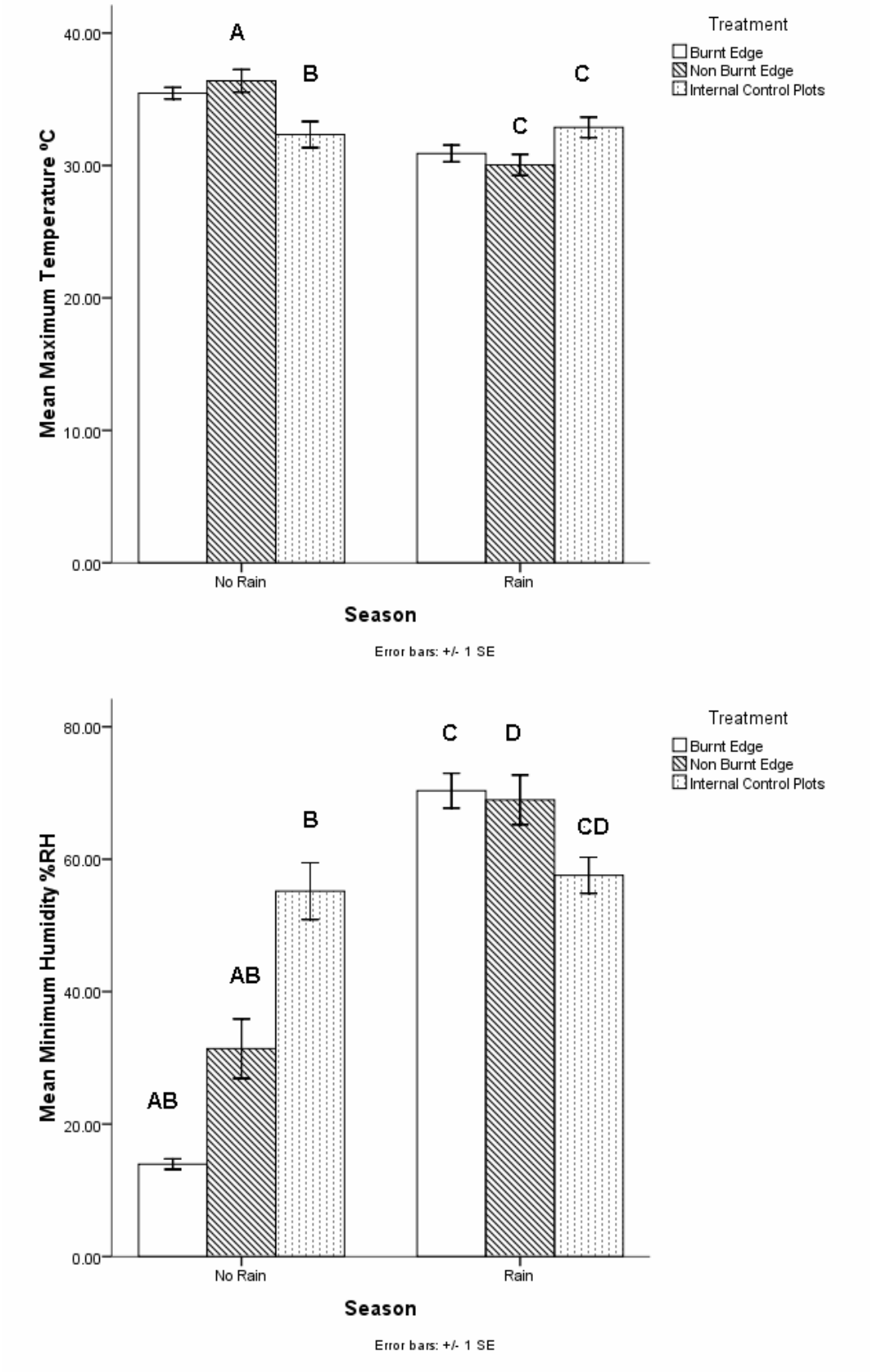


Fig 5.6. Differences in environmental parameters between seasons and treatment areas. Kwano forest. A, B, C and D represent significantly different groups.

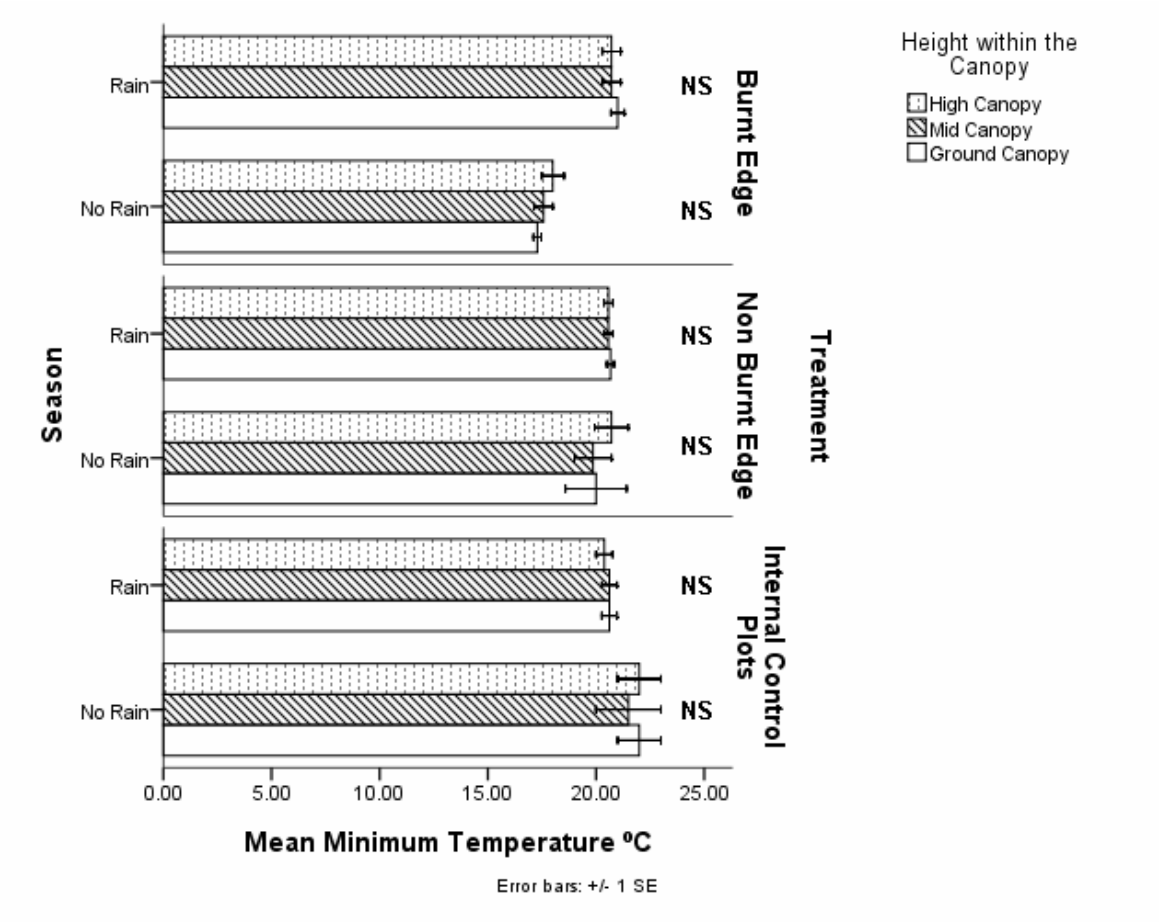
To investigate potential differences in environmental factors between heights, treatment and season the data were split, first by treatment (burnt, non burnt and internal control) and then by the presence of rain (rain and no rain). As data were normally distributed a one-way ANOVA with a Tukey post hoc test was used to analyse any potential difference in these environmental factors between heights.

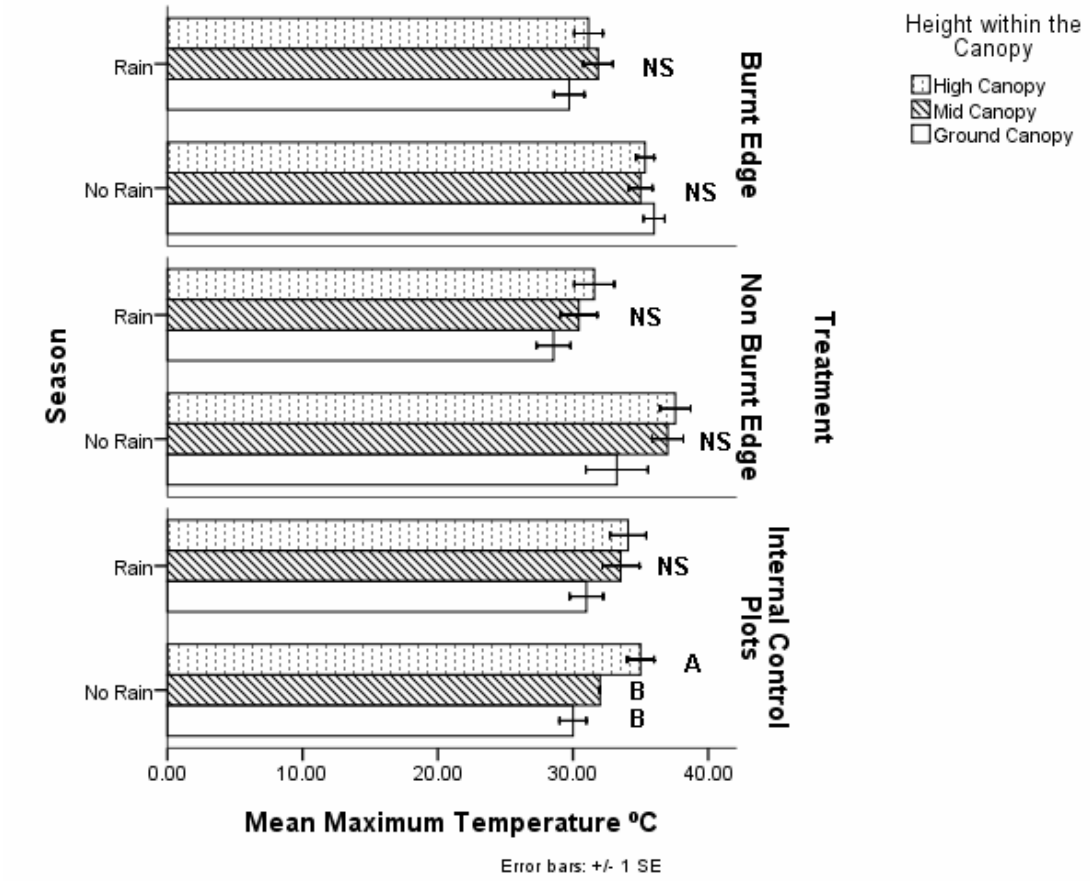
Neither minimum temperature, F (2, 19) = 0.82, *ns*, maximum temperature, F (2, 19) = 0.43, *ns*, or minimum humidity, F (2, 19) = 0.84, *ns*, showed any significant differences between heights at the burnt edge during dry periods. However during periods of rain at the burnt edge there was a significant difference between heights in the minimum humidity, F (2, 20) = 3.84, $p < 0.05$. Post hoc Tukey tests showed that the ground canopy had a significantly higher minimum humidity than the mid canopy, $p < 0.05$. Minimum temperature, F (2, 20) = 0.18, *ns*, and maximum temperature, F (2, 20) = 0.99, *ns*, showed no significant differences within the ANOVA model at the burnt edge during periods of rain (see fig 5.7, below).

At the non burnt edge minimum temperature, maximum temperature and minimum humidity showed no significant difference between heights during periods of no rain, F (2, 17) = 0.26, *ns*, F (2, 17) = 2.253, *ns*, and F (2, 17) = 1.015, *ns*, respectively. Nor did they show any significant differences between heights during periods of rain, F (2, 22) = 0.092, *ns*, F (2, 22) = 1.315, *ns*, and F (2, 22) = 1.349, *ns*, respectively.

In the internal control plots there was no significant differences among heights in minimum temperature, F (2, 5) = 0.059, *ns*, or in minimum humidity, F (2, 5) = 1.089, *ns*, during periods of no rain. However there was a significant difference in maximum temperature, F (2, 5) = 9.5, $p < 0.05$, in periods of no rain. Tukey post hoc analysis showed that the high canopy had significantly higher maximum temperatures than the

ground canopy, $p < 0.05$. There was no significant differences in any environmental parameters during periods of rain, F (2, 38) = 0.136, *ns*, F (2, 38) = 1.556, *ns*, and F (2, 38) = 1.111, *ns*, for minimum temperature, maximum temperature and minimum humidity respectively. Figure 2.7, below illustrates the differences in environmental parameters within the three treatment areas.




Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Season
Rain
No Rain
NS
A
B
B
Burnt Edge
Non Burnt Edge
Internal Control Plots
Treatment
0.00
10.00
20.00
30.00
40.00
Mean Maximum Temperature ºC
Error bars: +/- 1 SE

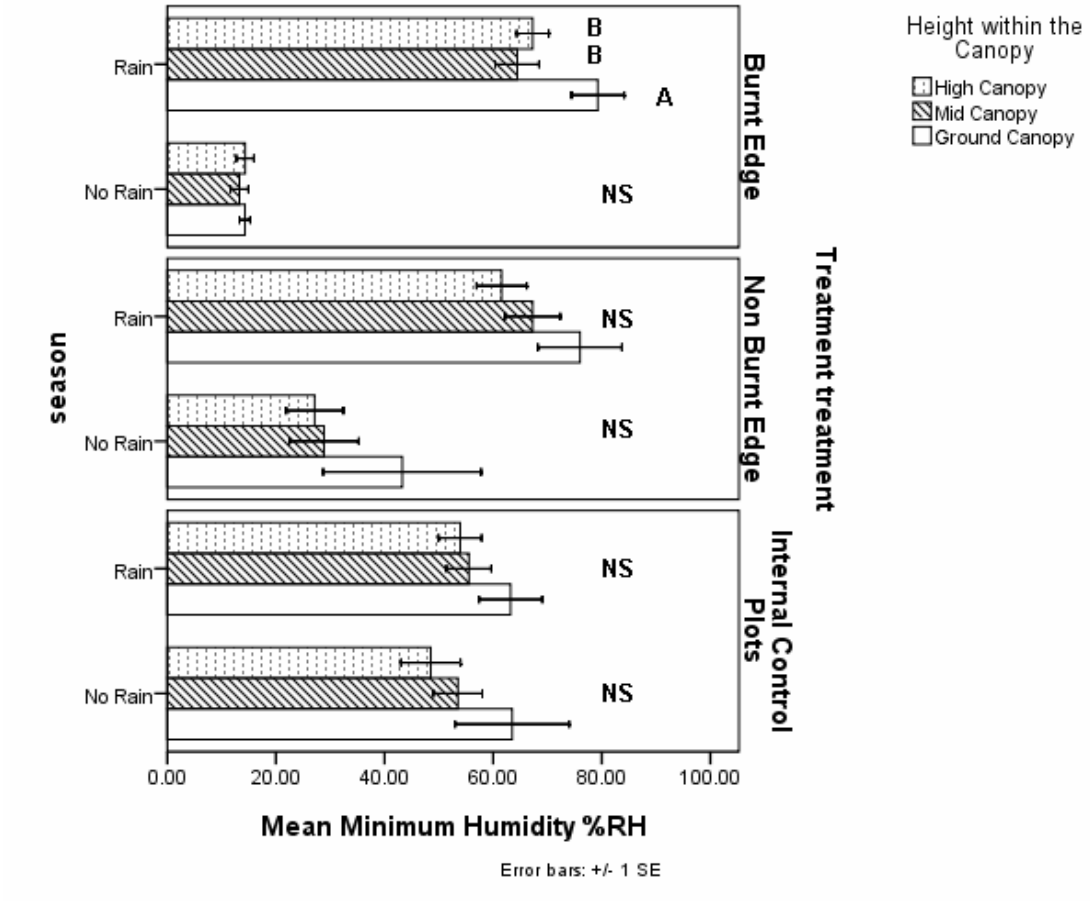

Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
season
Rain
No Rain
NS
A
B
B
Burnt Edge
Non Burnt Edge
Internal Control Plots
Treatment treatment
0.00
20.00
40.00
60.00
80.00
100.00
Mean Minimum Humidity %RH
Error bars: +/- 1 SE

Fig 5.7. Differences in environmental parameters between treatment areas, heights and periods of rain and no rain, Kwano forest. NS denotes no significant difference between heights, A and B = significantly different height groups.

It is at this point that the problem with the timing of the environmental data is evident. Internal control plots measured at the end of the dry season experienced quite a lot of rain; therefore there are very few data points in which to fit this analysis. As can be seen from the above figure the results for maximum temperature and minimum humidity are almost identical between periods of rain and no rain, as a result of this overlap in seasons. Therefore the environmental results from the internal control plots have been discounted from this point and only the burnt and non burnt edge are analysed in greater detail.

A one-way ANOVA was then used to investigate changes in these environmental parameters between periods of rain and no rain in the two treated edges. As there are only two groups to compare no Tukey post hoc analysis was needed.

Within the ground canopy there were significant differences in all parameters at the burnt edge, with minimum temperature, F (1, 13) = 106.74, $p < 0.001$ and minimum humidity, F (1, 13) = 171.81, $p < 0.001$ all increasing once the rains had come, and maximum temperature decreasing significantly during the rains, F (1, 13) = 20.89, $p < 0.001$. However in the non burnt edge there was no significant difference in minimum temperature, F (1, 12) = 0.52, *ns*, maximum temperature, F (1, 12) = 3.79, *ns*, or minimum humidity, F (1, 12) = 4.78, *ns*, between periods of rain and no rain (see fig. 5.7 above).

In the mid canopy burnt edge samples a similar pattern to the ground canopy burnt edge was found, with minimum temperature, F (1, 13) = 27.40, $p < 0.001$, and minimum humidity, F (1, 13) = 137.47, $p < 0.001$, both increasing during the rains and the maximum temperature decreasing during the rains, F (1, 13) = 5.01, $p < 0.005$. However unlike the

ground canopy, the mid canopy non burnt edge did show a significant decrease in maximum temperature, F (1, 13) = 13.56, $p < 0.005$ and a significant increase in minimum humidity, F (1, 13) = 22.17, $p < 0.001$, but there was no significant difference in minimum temperature, F (1, 13) = 0.66, *ns* (see fig. 5.7 above).

As with the ground and mid canopy at the burnt edge, the high canopy also shows minimum temperature increasing, F (1, 12) = 16.97, $df = 1$, $p < 0.005$, maximum temperature decreasing, F (1, 12) = 10.37, $p < 0.01$, and minimum humidity increasing, F (1, 12) = 225.06, $p < 0.001$, during the rains. Similarly the high canopy at the non burnt edge follows the same pattern as the mid canopy under this treatment with no significant difference in minimum temperature, F (1, 13) = 0.03, *ns*, but with maximum temperature decreasing, F (1, 13) = 10.40, $p < 0.01$ and minimum humidity increasing, F (1, 13) = 24.09, $p < 0.001$, during the rains (see fig 5.7 above).

None of the wet season environmental parameters showed any significant differences between treatment groups. In the ground canopy during periods of no rain only minimum humidity showed a significant difference between the two edge treatments, F (1, 12) = 8.33, $p < 0.01$, with the non burnt edge having a higher %RH, $p < 0.05$ (Tukey post hoc). The dry mid canopy showed no significant differences between the burnt and non burnt edges in any of the environmental parameters. In the dry high canopy minimum temperature, F (1, 14) = 5.92, $p < 0.05$, which was higher in the non burnt edge, $p < 0.05$ (Tukey post hoc) (see fig 5.7 above).

There is the possibility that there are other factors that are dictating the differences in environmental conditions between the two edges. Therefore the density of the habitat will also be analysed here. In section 2.3.6 the log average distance to the nearest vegetation was introduced as an explanatory variable. Here a possible relationship between this and

the environmental parameters will be analysed so to determine if it is in fact the treatment of the adjacent savannah causing these differences in abundance and community of Diptera and the environmental variables, or that there is a simple differences between two distinct patches of forest.

Pearson correlations between the log transformed total distances to vegetation and environmental parameters were performed. The only environmental correlate of log vegetation distance was with maximum temperature, $R = 0.206$, $p < 0.05$.

There was a significant difference indicated in the ground canopy, F (2, 37) = 12.45, $p < 0.001$. Tukey post analysis showed that the burnt edge vegetation distance was significantly greater than the non burnt edge, $p < 0.001$ (Tukey post hoc), and that the internal control plot distance to vegetation was also significantly greater than the non burnt edge, $p < 0.001$. There was no significant difference in the mid canopy between any of the treatment classes, F (2, 37) = 1.47, *ns*. In the high canopy there was a significant differences between treatments, F (2, 37) = 9.04, $p < 0.001$, however these significant difference were between the internal control plots and the burnt edge, $p < 0.005$ (Tukey post hoc) and the internal control plots and the non burnt edge, $p < 0.005$ (Tukey post hoc), both of which were smaller than the internal control plot. Figure 5.8, below, shows these differences.

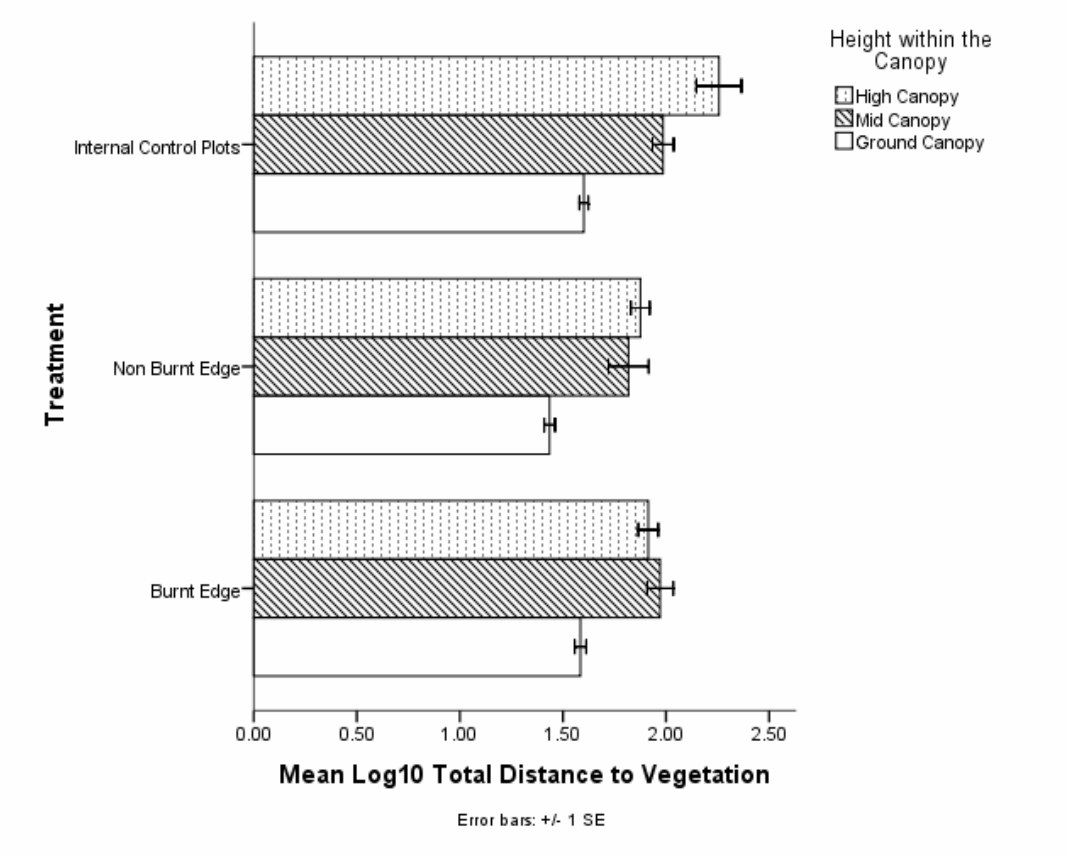
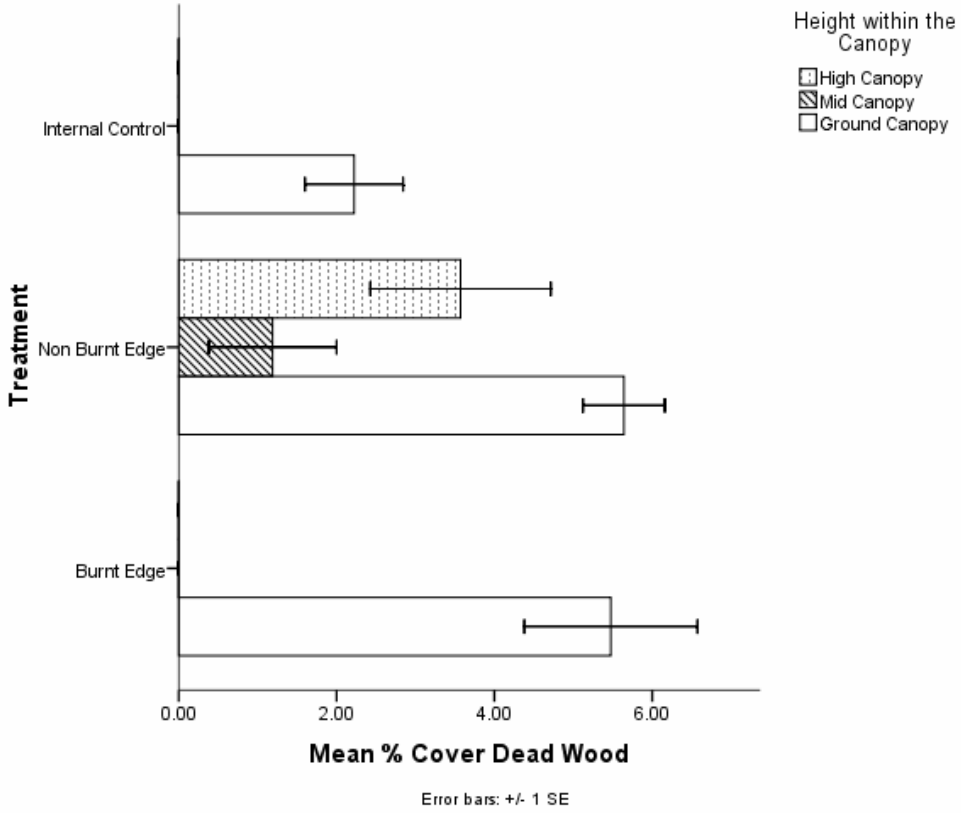
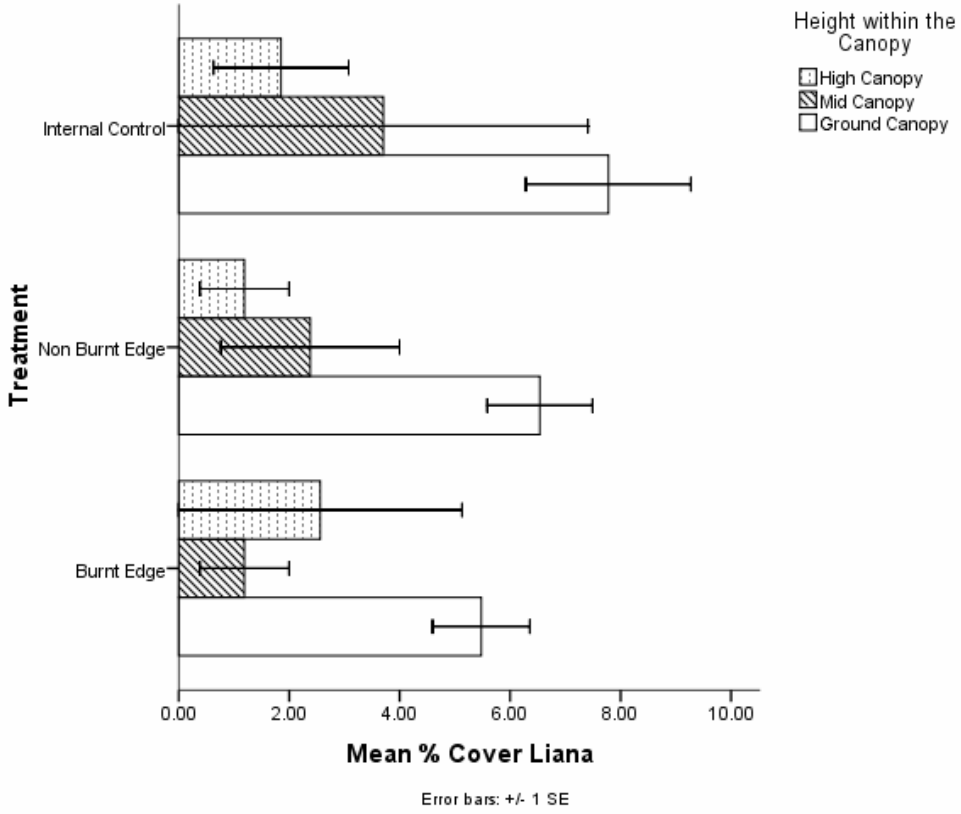
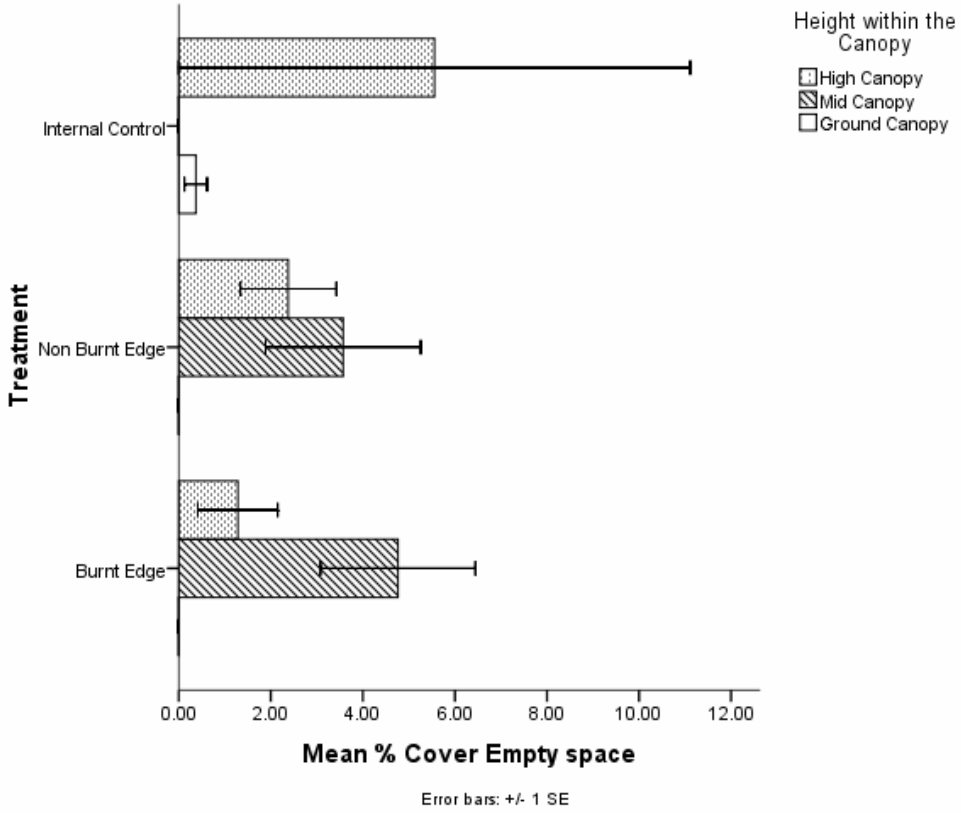


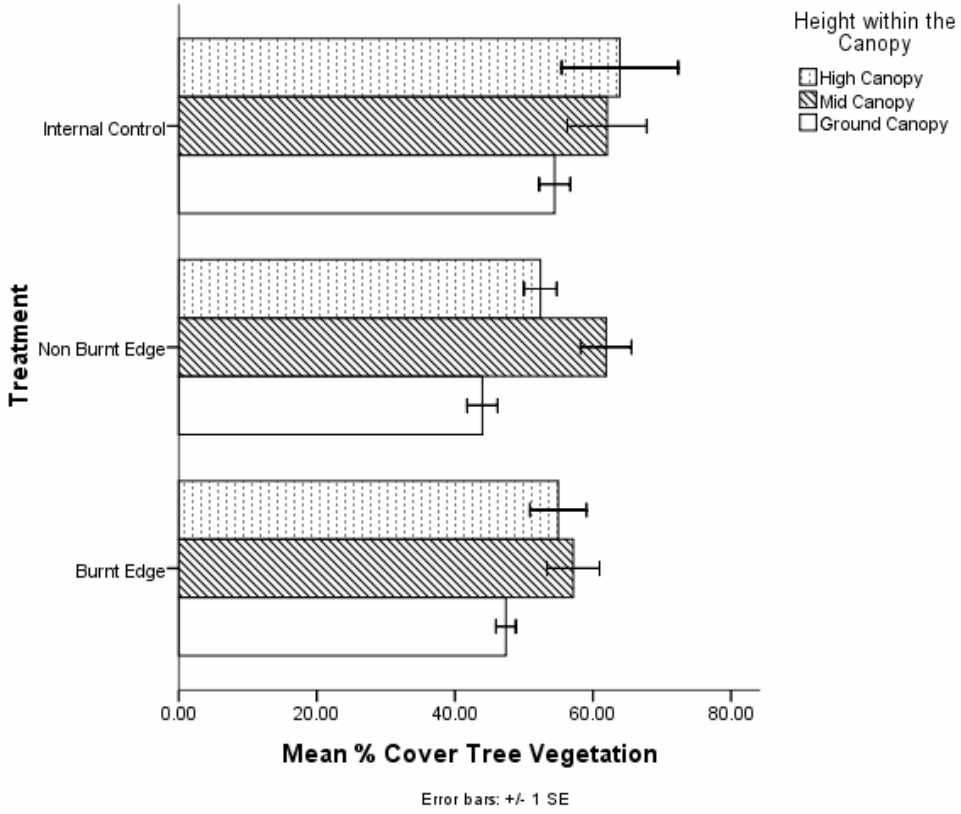
Fig 5.8. Difference between vegetation distances (m) in the three treatment areas, Kwano forest.

The percentage cover of vegetation type was also analysed between the two edges. A Mann-Whitney U test was used to analyse potential differences between the two edge habitats. The variables investigated were % cover of liana, tree vegetation (leaves), woody element, dead wood and empty space (defined as no element within 50 m of data point). Data were split by height class using treatment as the independent factor. In the ground and mid canopy there were no significant differences in vegetation types between burnt and non burnt edges. In the high canopy there was a significantly lower percentage cover of dead wood in the burnt edge, $z = -2.626$, $p < 0.01$, with no other significant differences within vegetation types between burnt and non burnt edges. Figure 5.9, below, illustrates these results.


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Treatment
Internal Control
Non Burnt Edge
Burnt Edge
0.00
2.00
4.00
6.00
Mean % Cover Dead Wood
Error bars: +/- 1 SE


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Treatment
Internal Control
Non Burnt Edge
Burnt Edge
0.00
2.00
4.00
6.00
8.00
10.00
Mean % Cover Liana
Error bars: +/- 1 SE


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Treatment
Internal Control
Non Burnt Edge
Burnt Edge
0.00
2.00
4.00
6.00
8.00
10.00
12.00
Mean % Cover Empty space
Error bars: +/- 1 SE


Height within the Canopy
High Canopy
Mid Canopy
Ground Canopy
Treatment
Internal Control
Non Burnt Edge
Burnt Edge
0.00
20.00
40.00
60.00
80.00
Mean % Cover Tree Vegetation
Error bars: +/- 1 SE

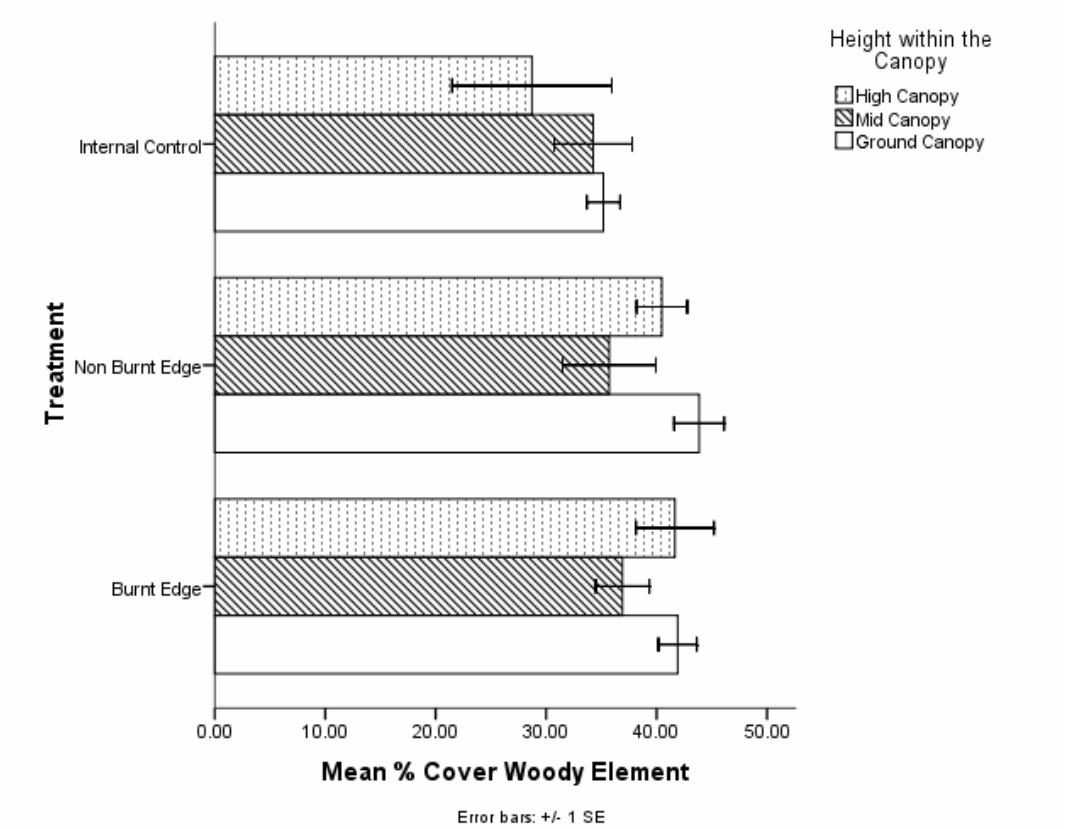


Fig 5.9. Differences in % cover (360º horizontal) of vegetation within heights and between treatments, Kwano forest.

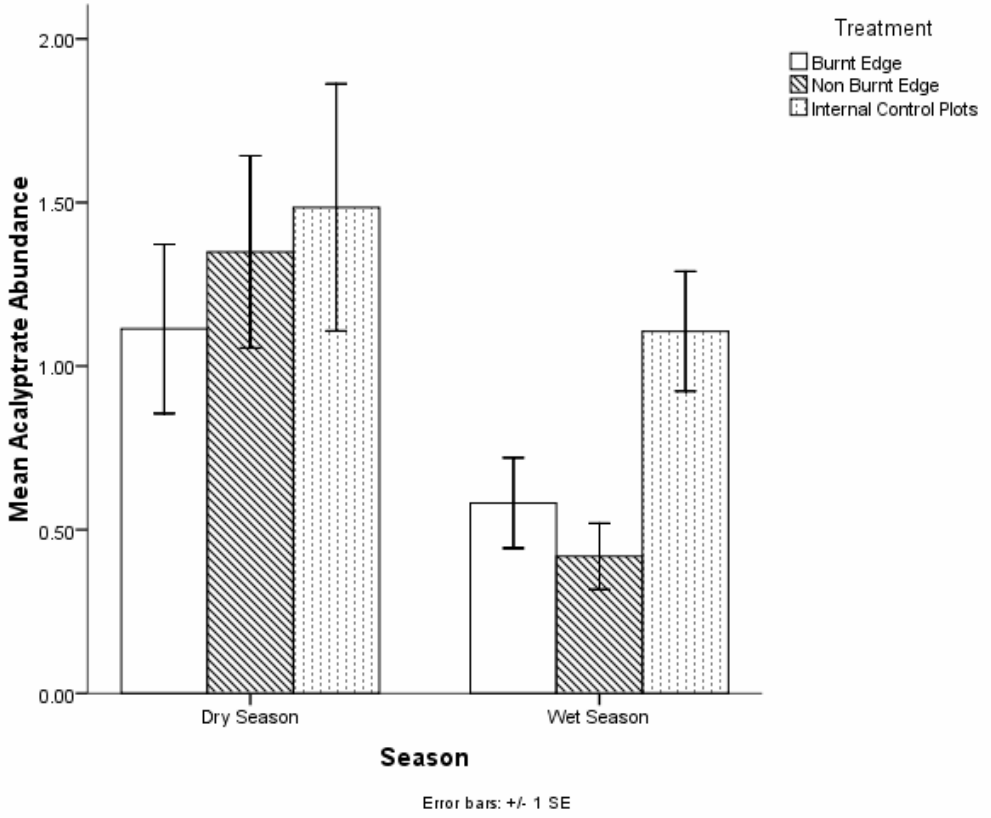
5.3.3 Effect of burning adjacent savannah on forest edge Diptera abundance and community structure

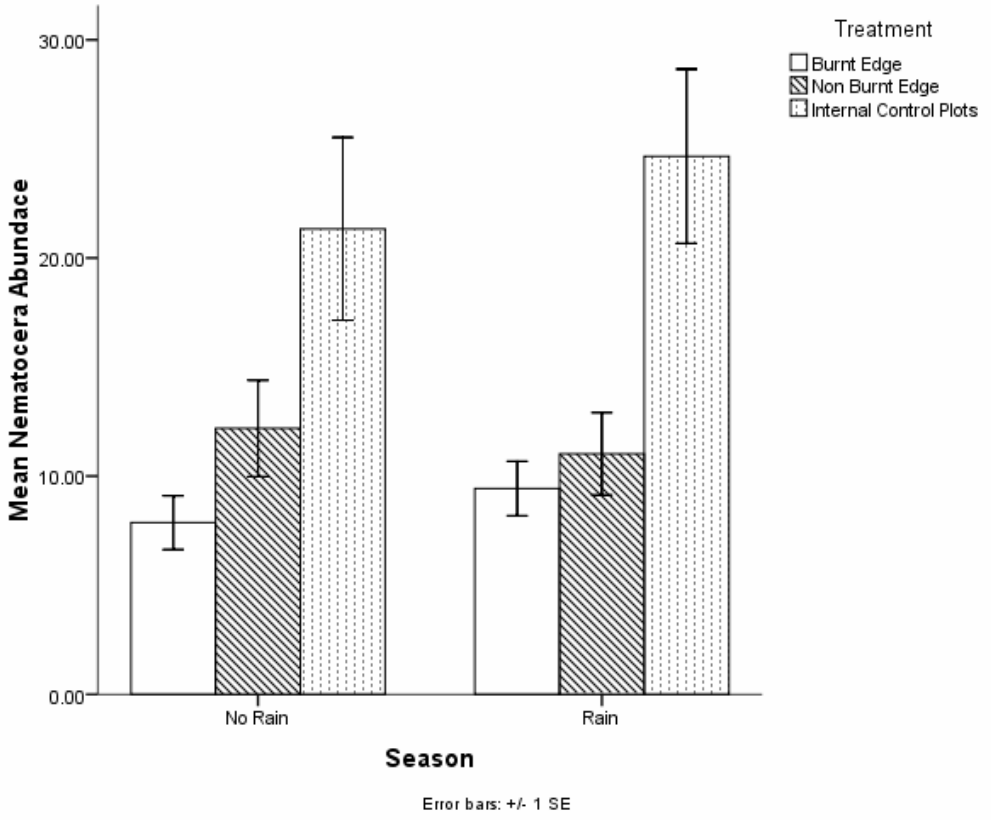
In the initial analysis no overall difference in Diptera abundance was seen between forest edges adjacent to burnt savannah and those adjacent to non burnt savannah in either season (see Chapter 3). Here the differences within groups and specific families will be discussed in further detail.

Initially all the data from the three treatment areas were grouped together, without taking height or distance (except for that of the internal control plots) into account. Only

nematoceran abundance data was normally distributed once naturally log transformed, therefore non parametric tests were used for all non transformed data for consistency. Unlike the savannah data, the forest areas have been split into three treatments, burnt edges, non burnt edges and internal control plots (>100 m from the edge). Therefore these three areas will be compared statistically. In the first instance the within season differences between treatments were compared using a Kruskal-Wallis test which showed that the Nematocera had significantly different abundances between treatments in the dry season ($H = 8.53$, $df = 2$, $p < 0.05$), whereas Acalyptrate ($H = 2.60$, $df = 2$, *ns*), Brachycera ($H = 3.085$, $df = 2$, *ns*) and Calyptrate ($H = 4.08$, $df = 2$, *ns*) did not show significance. Post hoc analysis was completed on Nematoccera using a Mann-Whitney test with a Bonfferoni corrected p value of 0.016 to avoid type 1 errors. Nemotocera showed significant differences between treatments, with a significantly higher abundance in dry season in the internal control plots compared to the burnt edge, $z = -2.925$, $p < 0.005$, and in the wet season with internal control plots again having higher abundance, but against both burnt, $z = -3.71$, $p < 0.001$, and non burnt edges, $z = -3.425$, $p < 0.005$ (see fig. 5.10 below).

A second Mann-Whitney test was conducted this time to look for seasonal changes within each of the treatment plots. As only one comparison was being made between treatments no correction of the p value was necessary. Here only the Calyptrate showed a significant difference with wet season abundances at the burnt edge, $z = -2.30$, $p < 0.05$, and non burnt edge, $z = -2.536$, $p < 0.05$, both decreasing from the dry season. Figure 5.10, below, illustrates these results.


Treatment
Burnt Edge
Non Burnt Edge
Internal Control Plots
Mean Acalyptrate Abundance
2.00
1.50
1.00
0.50
0.00
Dry Season
Wet Season
Season
Error bars: +/- 1 SE


Treatment
Burnt Edge
Non Burnt Edge
Internal Control Plots
Mean Nematocera Abundace
30.00
20.00
10.00
0.00
No Rain
Rain
Season
Error bars: +/- 1 SE

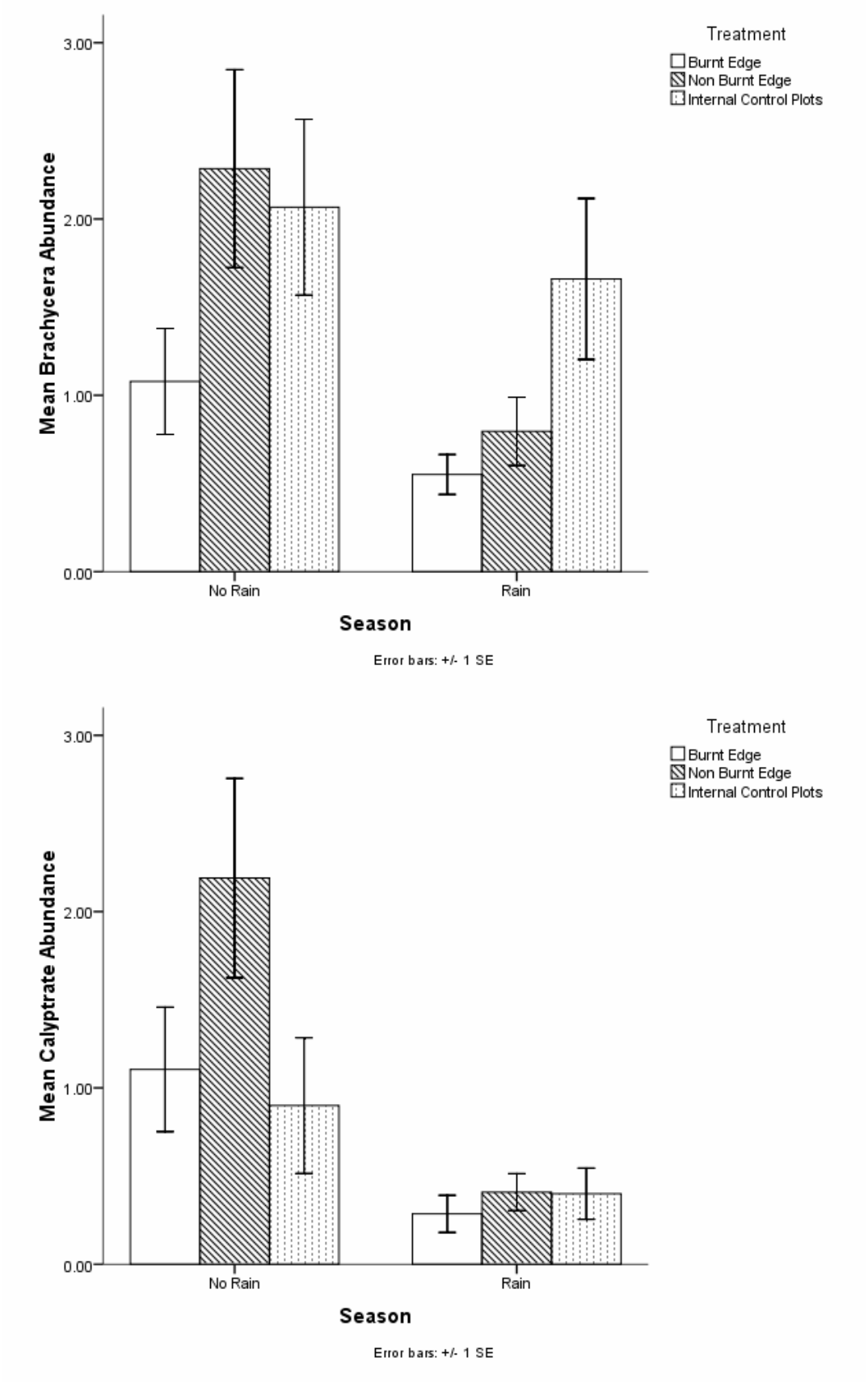
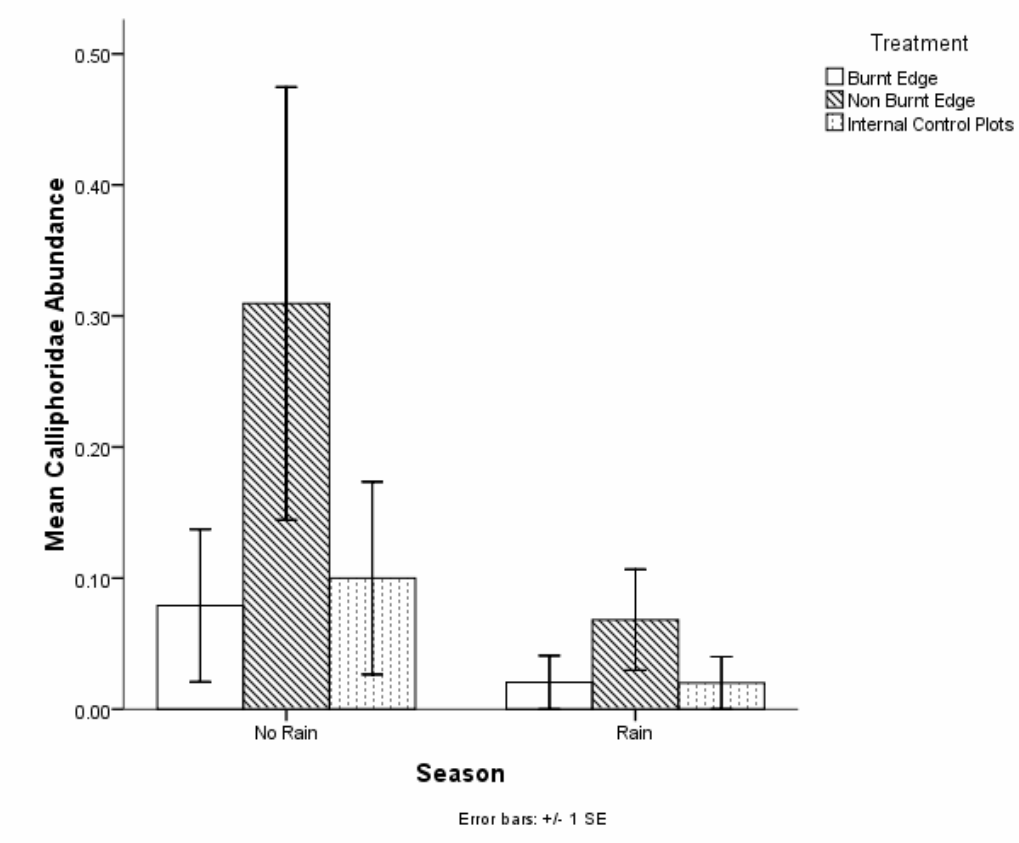
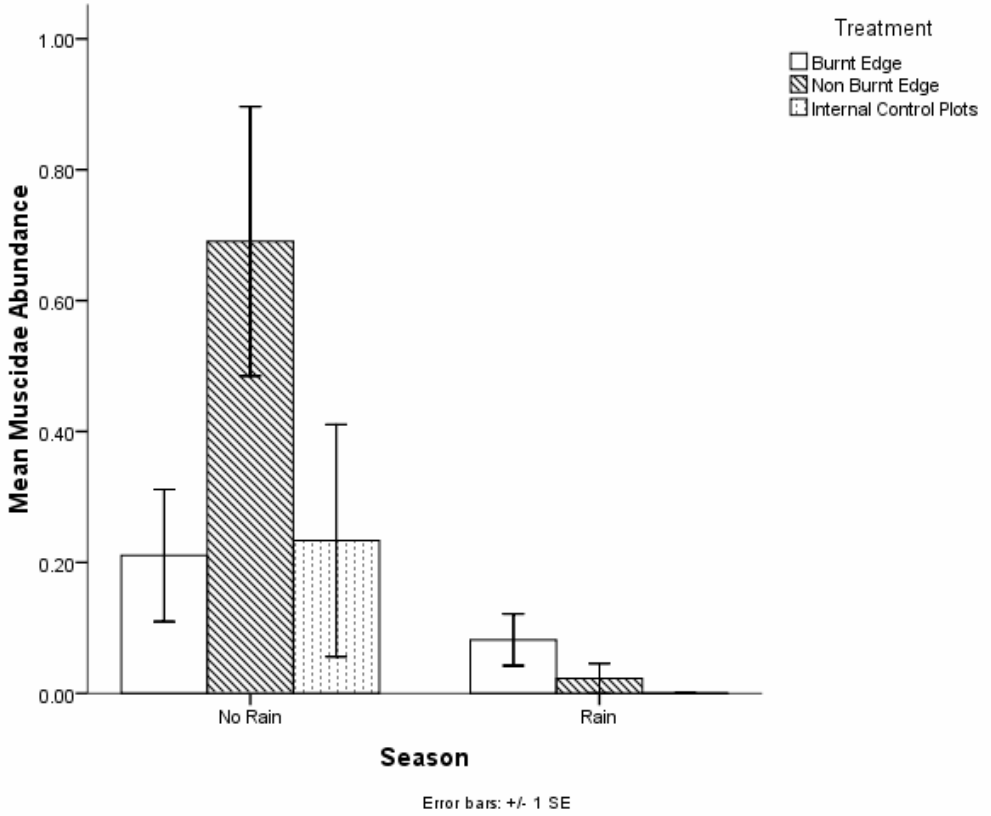


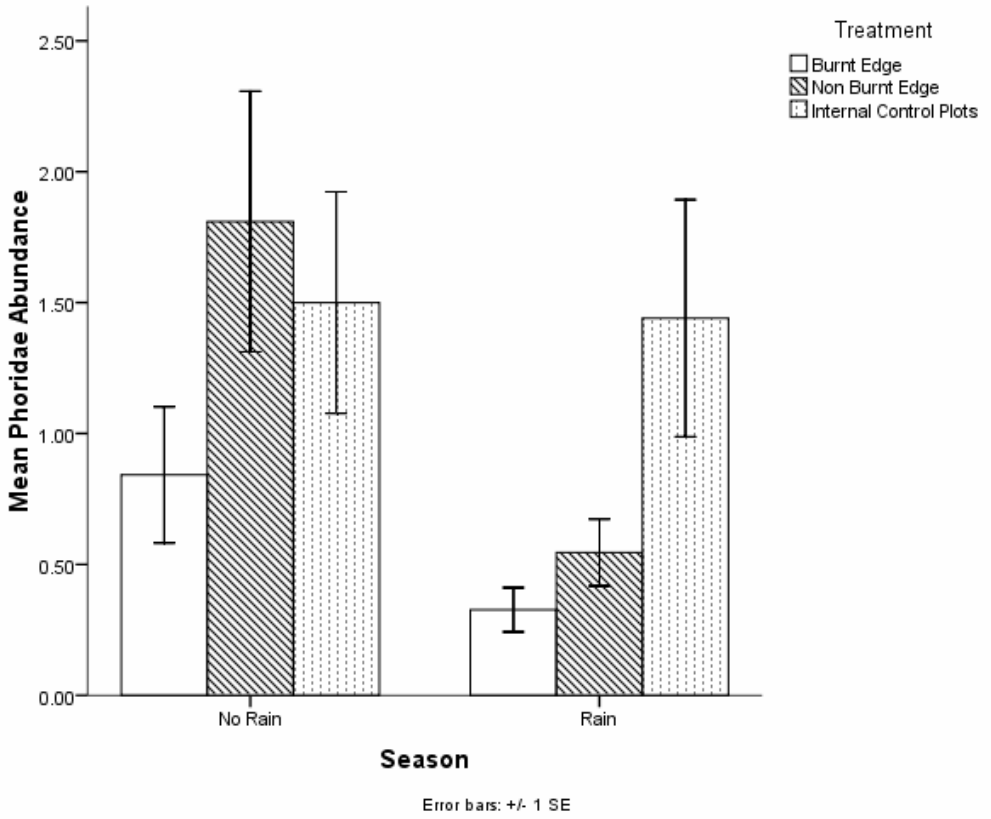
Fig 5.10, Differences in abundance (per trap day) of four sub orders of Diptera between treatment types and seasons, Kwano forest.

From figure 5.1, above, we can see that there is no significant reaction to burning in the savannah by Nematocera species in the edge plots; however the Calyptrates and the Brachycera are showing a trend in their preferences, especially in the dry season (immediately post burn). Therefore a selection of family abundances from these two sub orders were analysed in greater detail, these were; Sarcophagidae, Muscidae, Tachinidae, Calliphoridae (all Calyptrate) and Phoridae (Brachycera).

The Kruskal-Wallis analysis for periods of no rain showed that only the Muscidae had significantly different abundances within the treatment classes analysed (H = 7.568, df = 2, $p < 0.05$) and in the periods of rain only the Phoridae showed significant differences (H = 6.524, df = 2, $p < 0.05$). Muscidae and Phoridae abundance were tested with post hoc Mann-Whitney tests using a Bonferroni corrected p value of 0.016, and only Phoridae showed a significantly high abundance during periods of rain compared to the burnt edge,, z = -2.51, $p < 0.016$. Figure 5.11, below, shows the trends in the data.




Treatment
Burnt Edge
Non Burnt Edge
Internal Control Plots
Mean Muscidae Abundance
1.00
0.80
0.60
0.40
0.20
0.00
No Rain
Rain
Season
Error bars: +/- 1 SE


Treatment
Burnt Edge
Non Burnt Edge
Internal Control Plots
Mean Phoridae Abundance
2.50
2.00
1.50
1.00
0.50
0.00
No Rain
Rain
Season
Error bars: +/- 1 SE

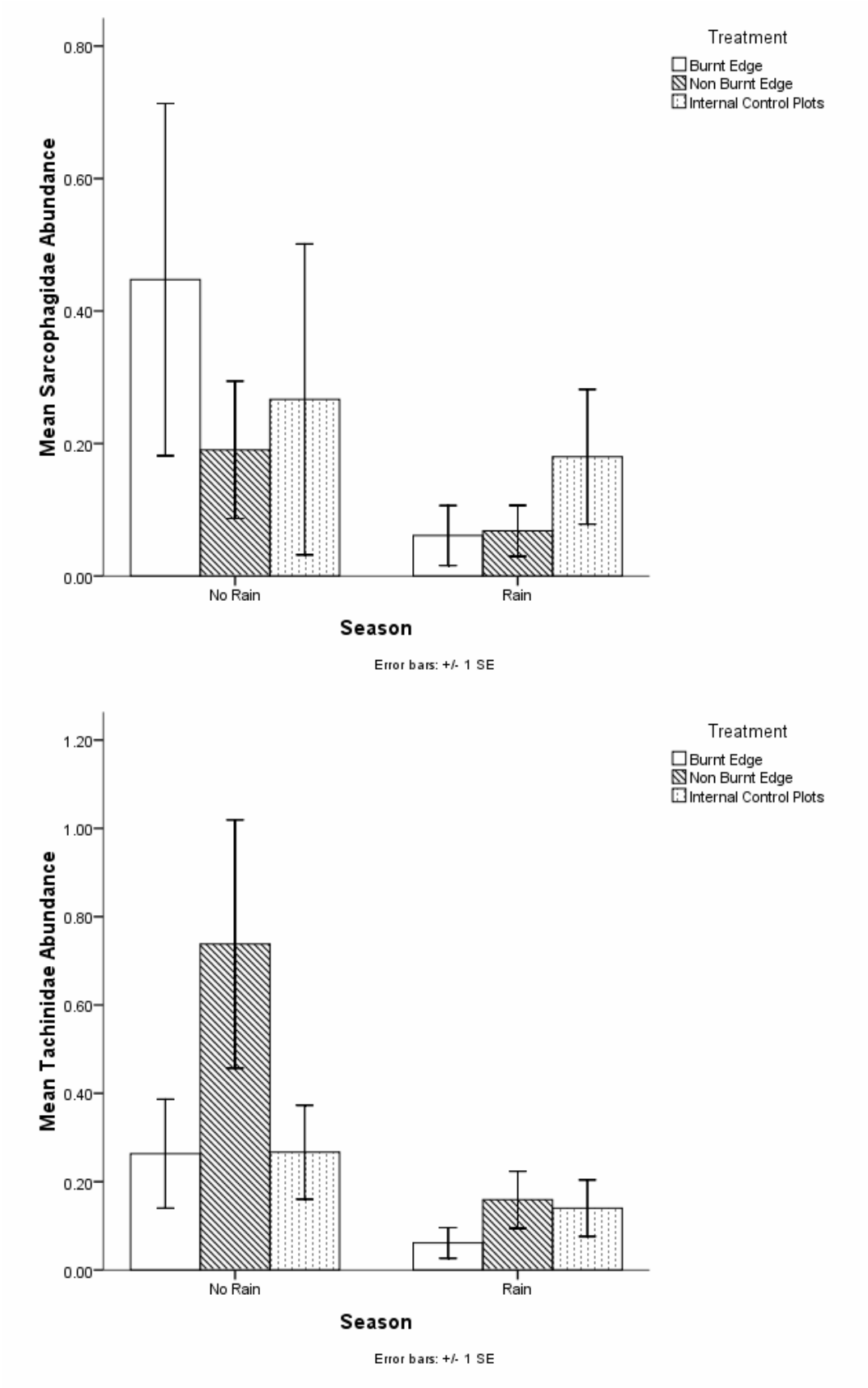


Fig 5.11. Abundances (per trap day) of five Caltptrate families in the burnt, non burnt and internal control plots, Kwano forest.

The results of the non parametric ANOVA and post hoc tests are slightly frustrating as there are clear patterns in the data, especially in the Muscidae, Tachinidae, Calliphoridae and Phoridae, who are all showing an affinity with the non burnt edge of the forest during dry periods; whereas the Sarcophagidae are more abundant at the burnt edge during the same periods. As has been shown previously the Calyptrate abundance drops dramatically during the rains, but here we can see that the Phoridae abundance only drops towards the edge of the forest (both edge treatments) but maintains its abundance in the internal control.

As these statistical results are not showing the trend of variation that is clearly present within the data a different statistical approach was used. Canonical correspondence analysis (CCA) was used to confirm the pattern seen in figure 5.11, above. Because of the nature of CCA analysis, all lines of data that contained zero individuals were removed from the dataset. Each treatment and season was given as its own variable. To do this each treatment or season was scored either as 1 or 0 depending on the site and time of year that the particular sample was taken. Therefore a total of three variables were entered into the CCA, these were; non burnt edge, burnt edge and wet season. The abundance data were transformed using a log transformation prior to analysis and rare species were down weighted, a Monte Carlo permutations test with 999 permutations was used to ascertain the contribution to variability that the variables were exerting on the data set. All Analysis was done using Canoco for Windows 4.5.

The CCA showed that 2 out of the 3 variables explained 18 % of the variation in the abundance. With the first axis explaining a majority of the relationship between the treatment and seasonal effects and the abundance data, $F = 11.36$, $p < 0.001$ (Monte Carlo test with 999 permutations), and the total inertia of the eigenvalues was 1.625. The CCA biplot of the first and second axis in figure 5.12, below, shows that the families that

trended towards the non burnt edges in the dry season (see figure 5.11), are all grouped together, with sarcophagidae (dry season burnt edge affiliation) and Phoridae (wet season internal control plot affiliation) are in separate groups.

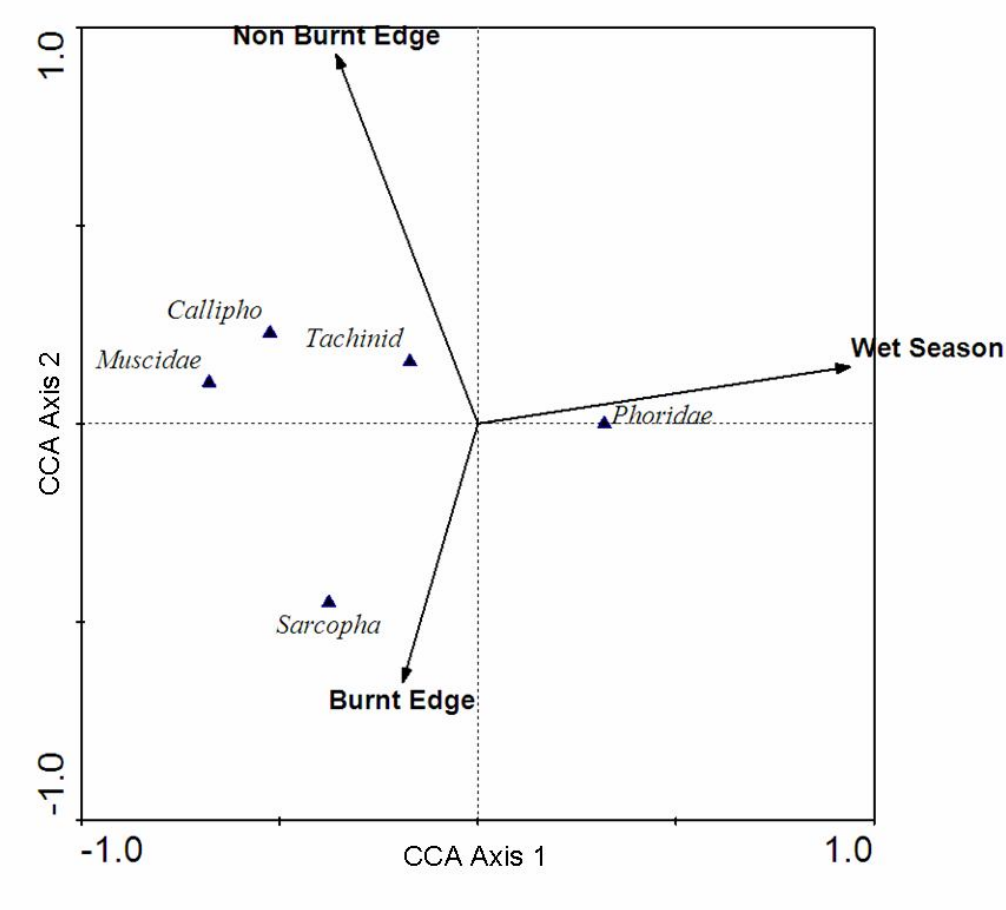


Fig 5.12. CCA biplot of treatment variables and family abundance (per trap day).

5.3.4 Variation in Diptera families due to treatment, height and rain

Data on changes to microclimate and their effect in Diptera family abundance have already been analysed within the vertical column; here, however, potential differences in the environmental conditions through the vertical column within different treatment zones will be analysed in greater detail. Families such as the Certopogonidae, Cecidomyiidae and Chironomidae were shown to be significantly affected by both height and changes in

season through the vertical column, so again these families will be studied in more detail. However the previous section also showed that families from both the Calyptrate and Brachycera were affected by treatment, therefore these families will also be included in this analysis.

Unlike the previous section the rain data used here is spread across both the 2009 and 2010 field seasons, therefore more 'no rain' data points are available within the internal control plots and these will be included within this section of analysis. The family abundance data was not normally distributed therefore non parametric ANOVA's with corrected post hoc tests were used.

The data were split by the presence of rain and treatment and then a Kruskal-Wallis test was used to investigate the differences in abundance of eight families, these were; Ceratopogonidae, Chironomidae, Cecidoyiidae, Phoridae, Muscidae, Sarcophagidae, Tachinidae and Calliphoridae. All these families have been shown previously to be affected by either height within the canopy or the treatment of the adjacent savannah.

In the dry burnt edge only Chironomidae ($H = 8.208$, $df = 2$, $p < 0.05$), Cecidomyiidae ($H = 14.99$, $df = 2$, $p < 0.005$) and Phoridae ($H = 7.145$, $df = 2$, $p < 0.05$) showed significant differences between ranks. During periods of rain only Ceratopogonidae ($H = 6.542$, $df = 2$, $p < 0.05$) and Chironomidae ($H = 6.168$, $df = 2$, $p < 0.05$) showed significant differences in the burnt edge (see fig. 5.13 (a-f) below).

Four families showed significant differences in the non burnt dry plots, there were; Ceratopogonidae ($H = 15.910$, $df = 2$, $p < 0.001$), Chironomidae ($H = 7.450$, $df = 2$, p ¸0.05), Cecidomyiidae ($H = 7.525$, $df = 2$, $p < 0.05$) and Muscidae ($H = 10.175$, $df = 2$, $p <$ 0.01). No other family showed any significance between ranks. During the rains the

Ceratopogonidae (H = 8.521, df = 2, $p < 0.05$), Chironomidae (H = 15.794, df = 2, $p < 0.001$), Cecidomyiidae (H = 13.760, df = 2, $p < 0.005$) and Calliphoridae (H = 6.083, df = 2, $p < 2$) showed significant differences.

Two families, Ceratopogonidae (H = 16.693, df = 2, $p < 0.001$) and Tachinidae (H = 10.755, df= 2, $p < 0.005$) showed significant differences in the dry internal control plots, no other family showed any significance. No family showed any significant differences in the internal control plots during the rains.

Post hoc Mann-Whitney tests with Bonferroni corrected p values of 0.016 to avoid type one errors were used to discover the nature of the significant differences shown in the non parametric ANOVA. At the burnt edge there was no significant difference in abundance between ground and mid canopy or the mid and high canopy during either the rain or no rain periods. There was also no significant difference in abundances between the ground and high canopy during periods of rain. There was, however a significantly higher abundance in the ground canopy compared to the high canopy in the Cecidomyiidae, z = -4.018, $p < 0.001$, and Phoridae, z = -2.674, $p < 0.01$, during dry periods.

The non burnt edge showed no significant difference in abundance of the studied families during periods of rain between the ground and mid canopy. Ceratopogonidae did show a higher abundance in the mid canopy during periods of no rain compared to both the ground, z = -3.029, $p < 0.005$, and the high canopy, z = -3.495, $p < 0.01$, and during periods of rain had a significantly higher abundance in the high canopy compared to the mid canopy, z = -2.780, $p < 0.01$. Chironomidae had a significantly higher abundance in the high canopy during the rains than the ground canopy, z = 2.939, $p < 0.005$, and the mid canopy, z = -3.558, $p < 0.01$. Cecidomyiidae showed a significantly higher abundance in the ground canopy compared to the high canopy during the dry periods, z = -2.592, $p <$

0.01, and a significantly higher abundance in the high canopy compared to the mid canopy, $z = -3.227$, $p < 0.01$, during wet periods.

In the internal control plots Ceratopogonidae had a significantly higher abundance in the mid canopy compared to the ground canopy, $z = -2.552$, $p < 0.01$, and in the high canopy compared to the mid canopy, $z = -3.719$, $p < 0.001$, during periods of no rain. Phoridae showed a significantly higher abundance in the high canopy compared to the ground canopy during the rains, $z = -3.176$, $p < 0.01$. Figure 5.13, below, illustrates the difference in abundance of the four families shown by this analysis.

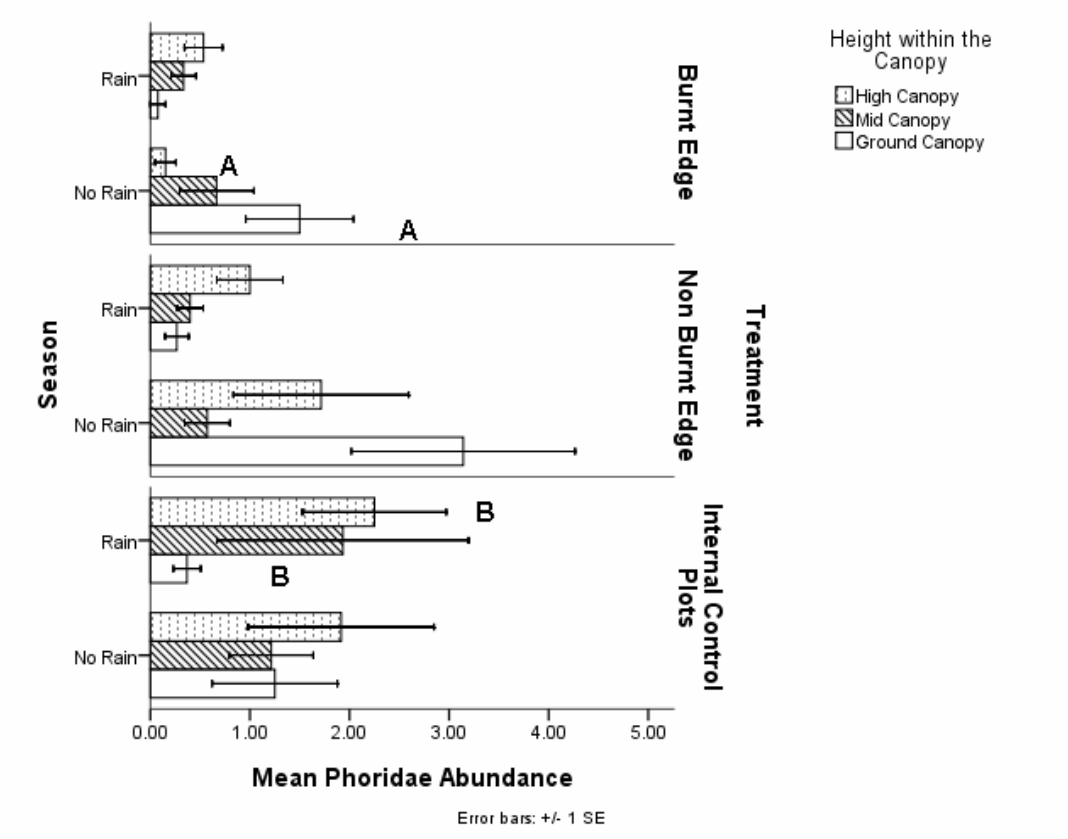


Fig 5.13 (a). Abundance (per trap day) of Phoridae by height, treatment and season. A and B = significantly different groups

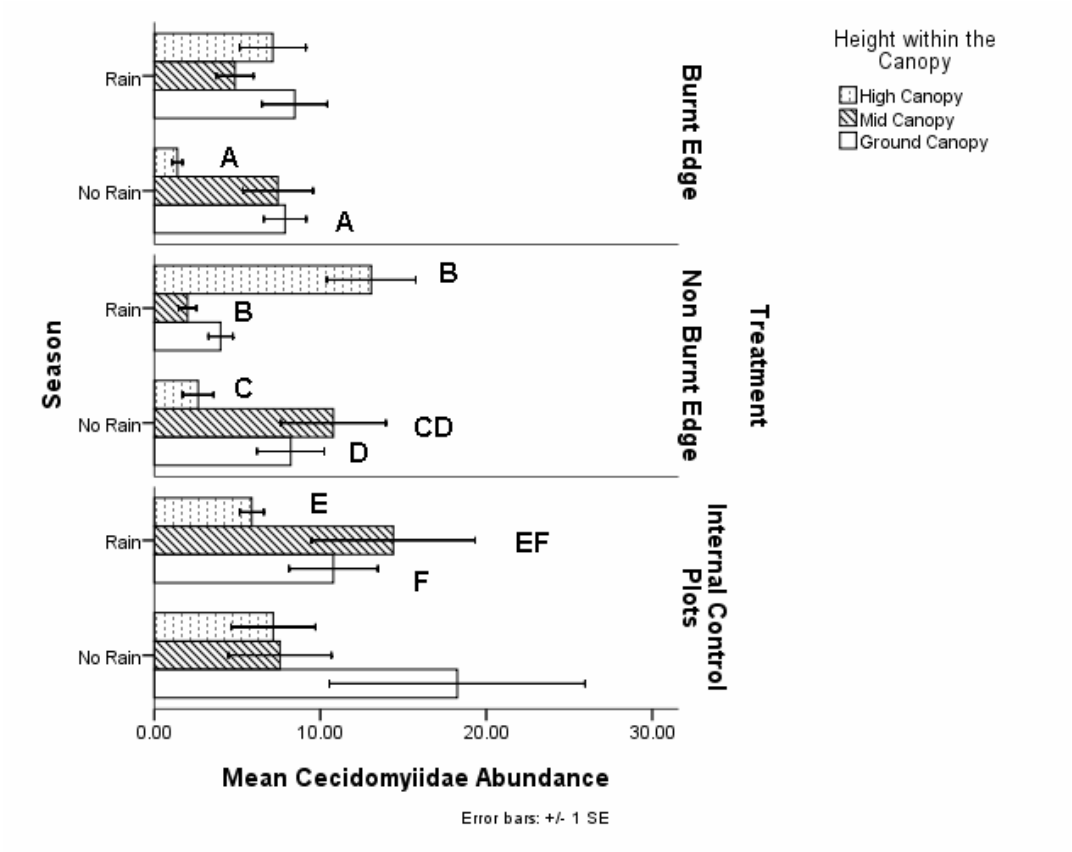


Fig 5.13 (b). Abundance (per trap day) of Cecidomyidae by height, treatment and season. A – F = significantly different groups.

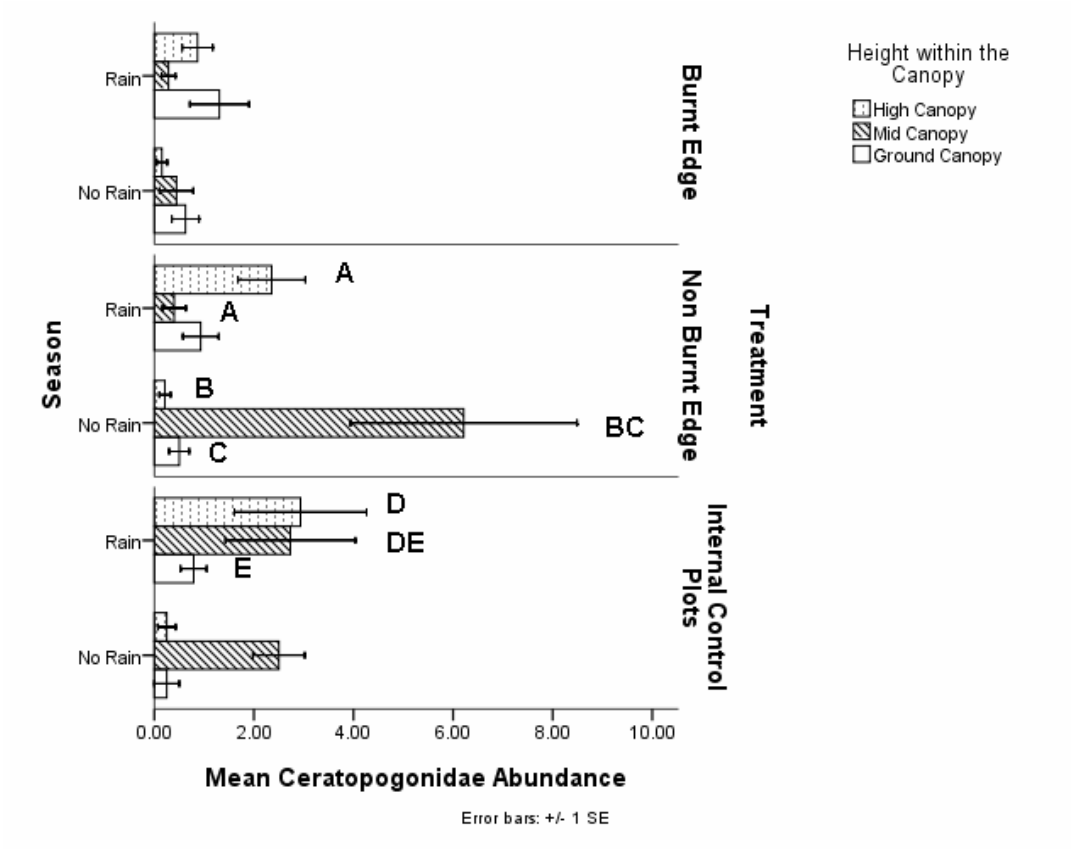


Fig 5.13 (c). Abundance (per trap day) of Ceratopogonidae by height, treatment and season. A – E = significantly different groups.

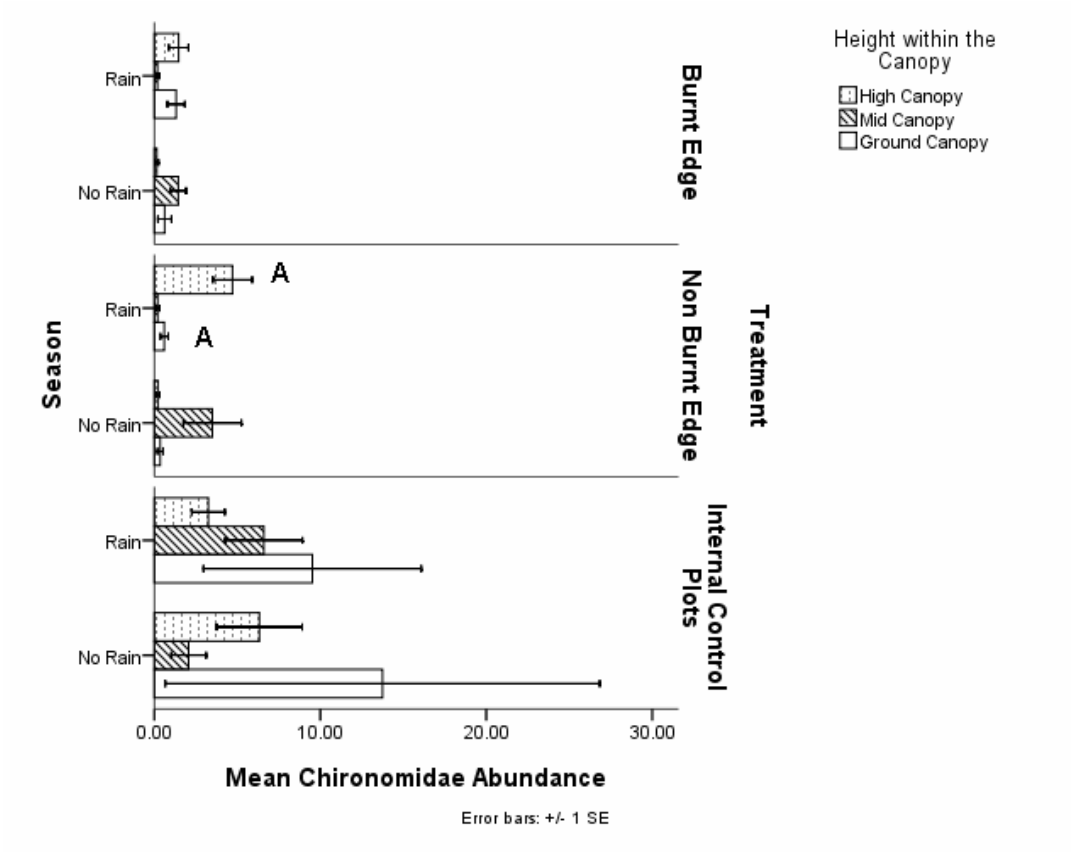


Fig 5.13 (d). Abundance (per trap day) of Chironomidae by height, treatment and season. A = significantly different groups

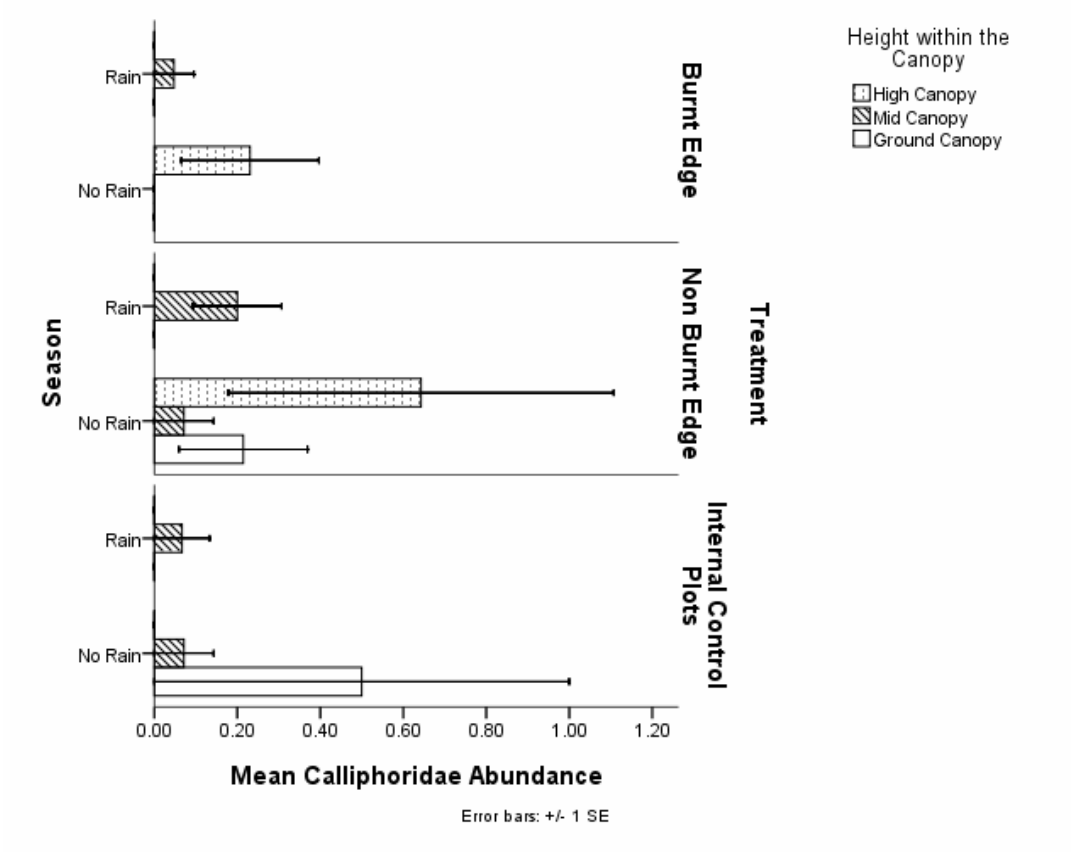


Fig 5.13 (e). Abundance (per trap day) of Calliphoridae by height, treatment and season, Kwano forest.

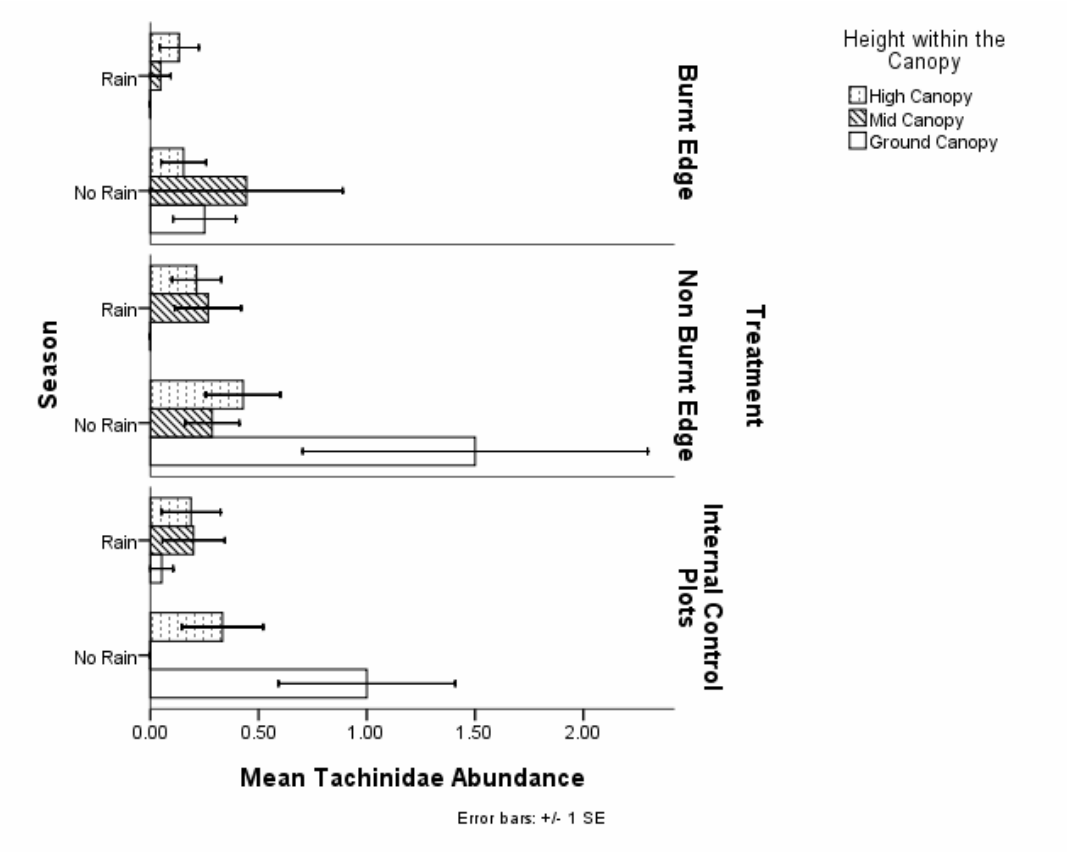


Fig 5.13 (f). Abundance (per trap day) of Tachinidae by height, treatment and season, Kwano forest.

To determine if there were significant differences in abundances in the target families between treatment groups within heights and seasons the data was first split in by the presents of rain and height category. Initially a Kruskal-Wallis test was conducted on all eight families to determine if there were significant differences between ranks.

The results from the ground canopy showed no significant differences in any of the families in either seasonal period between the treatment groups. Results from the mid canopy showed that during dry periods the Ceratopogonidae had significant differences between treatments ($H = 10.134$, $df = 2$, $p < 0.01$). Taking into account a Bonferroni corrected p value of 0.016, Mann-Whitney post hoc analysis showed there to be a higher abundance in the non burnt areas than the burnt areas, $z = -2.701$, $p < 0.01$, and a higher abundance in the internal control plots than the burnt areas, $z = -3.019$, $p < 0.005$. During the rains both the Chironomidae ($H = 6.504$, $df = 2$, $p < 0.01$) and Cecidomyiidae ($H =$

12.314, $df = 2$, $p < 0.005$) showed significant differences between ranks. After Bonferroni corrections there were in fact no significant differences between treatment groups in the Chironomidae; however, the Cecidomyiidae showed that there was a higher abundance in the internal control plots than in the burnt edge plots, z = -3.316, $p < 0.001$.

In the high canopy during periods of no rain the Chironomidae ($H = 6.504$, $df = 2$, $p < 0.05$) showed significance between treatments, however post hoc Bonferroni corrected Mann-Whitney tests showed there to be no significant differences between any of the treatment areas. During the rain the Phoridae, $H = 6.729$, $df = 2$, $p < 0.05$, were the only family to show any significant differences between treatments and the corrected Mann-Whitney post hoc tests revealed that the internal control plots had a significantly higher abundance than the burnt edge, $z = -2.573$, $p < 0.01$.

To help describe the pattern seen in the above analysis a CCA was performed on the eight Diptera families, using five variables to help explain the variation seen. The variables were made up of burnt and non burnt treatment zones, ground and high canopy height categories and wet season. As with the previous CCA analysis each variable was described as either a 1 or 0. The family abundance data were transformed using a log transformation before analysis, with Monte Carlo post hoc tests to describe the significance of each variable (999 permutations). All samples that had zero abundance were removed prior to analysis and rare species down weighted. As before all CCA analysis was conducted in Canoco 4.5 for Windows.

The total inertia of the data set was 1.232, and the variables explained 14 % of the variation within the data set with the first 6 explaining the majority, $F = 3.70$, $p < 0.05$. The first two axes explained 85 % of the relationship between the variables. Figure 5.14, below, shows the biplot from the CCA. The most striking feature of this biplot is that the

first axis is so closely aligned with the presence of rain in the habitat. The biplot shows again the grouping of Tachinidae, Calliphoridae, Sarcophagidae and Phoridae along the non burnt edge vector within periods of no rain, however there appears to be no close association with height classes. Muscidae are most closely associated with periods of no rain and the three Nematocera families tied with multiple factors.

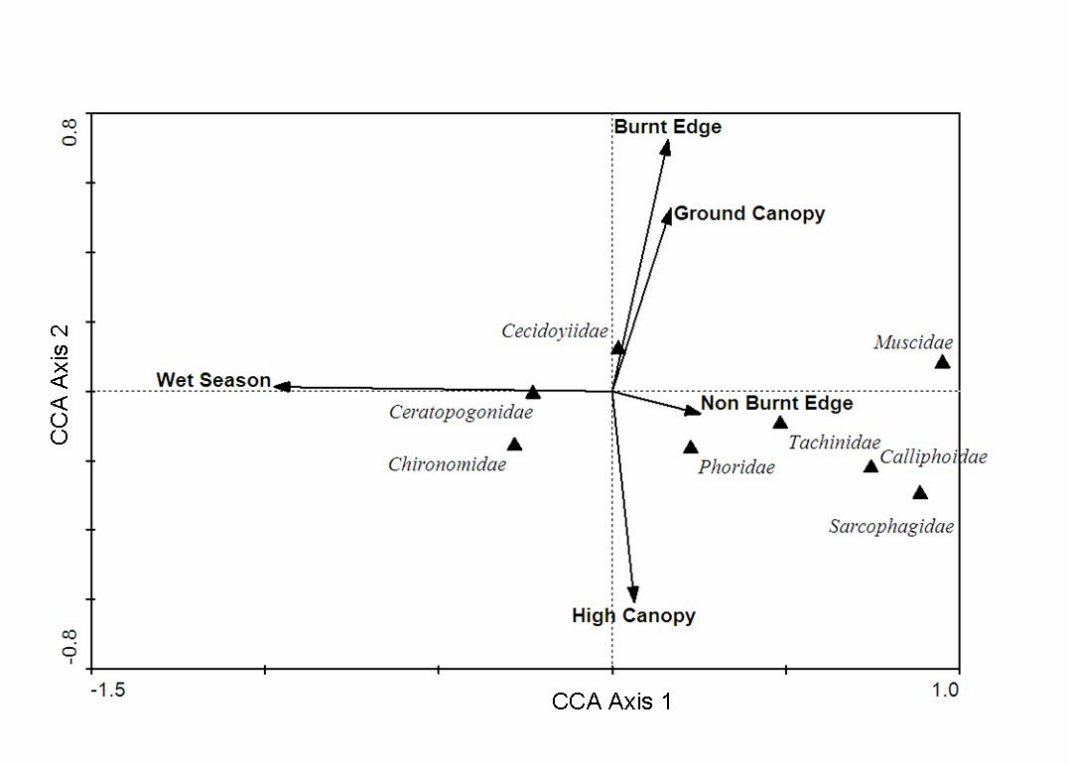


Fig 5.14. CCA biplot of seasonal, height and treatment affect on the abundance (per trap day) of eight families of Diptera.

5.4 Conclusions

The premise of this chapter was to establish if there was a detectable effect of burning treatment on Diptera abundance at the family level. Within the savannah itself the results showed that calyptrate families were affected, and although only the Muscidae showed a significant affect, the Sarcophagidae and Calliphoridae were also showing trends in the same direction. These trends pointed towards an affiliation towards the burnt savannah

with all three families increasing in abundance after the savannah was burnt. In the previous chapter the literature showed that these families were associated with dung and carrion, or in some cases other decaying organic material. However in the burnt savannah the habitat is very much made up of burnt organic vegetation, which is not a resource that these families are known to use. Larvae of these families are not known to emerge from the soil horizon of burnt areas.

This result also contrasts the results of authors such as Uys et al. (2006) who concluded that large bodied mobile invertebrates would decrease in an areas after a burn event either due to mortality or an increased propensity to disperse. The post burn samples were collected roughly four days after the savannah was burnt, which would not only allow time for families such as the ones analysed here to disperse away, but also to return. However we must ask if these families did return after the burn, why would they do so?

There were no observed carcases deposited in either savannah area, and there is no link towards Calyptrate individuals being attracted towards burnt carcases more than non burnt (see Chin et al (2008) for example). Therefore possible increased prevalence of resources can be ruled out as a probable cause. Possibly related is the observation that the Muscidae, Tachinidae and Calliphoridae abundances fell within the forest adjacent to the burnt forest edge. Although not significant within the non parametric ANOVA, CCA (see figs 5.13 and 5.14) analysis did point towards this conclusion. This would mean that these families were dispersing from the forest margins into the adjacent savannah once the burn had been conducted.

Possible explanations of the differences seen here and those concluded by Uys et al (2006) could be as fundamental as taxanomic variation. Uys et al. based their research on South African savannah systems, which are subject to differences in both climatic conditions and

fauna and flora to those, like the forest at Kwano, in the West Guinean Forests, there may also be differences in fire regimes practised in the two areas.

The possible differences seen between family abundances within the two treatment forest edges are also quite obvious. The analysis was careful to try to disqualify other possible factors that could have had an effect on the abundances seen. These factors were looked at in terms of the structure and density of the two forest edges which would have an effect on microclimate and in some cases resource availability within the habitat, and potential resources in terms of vegetation types available within the immediate vicinity of the sample site. The analysis first showed that there were distinct differences in environmental parameters between the burnt and non burnt edge of the forest, with minimum temperature and humidity being significantly lower in the burnt edge compared to the non burnt edge. Analysis of the distance to the nearest vegetation within each of the treatment areas showed that the non burnt edge had a significantly denser structure than both the bunt edge and internal control plot. This was indicated by its distance to nearest vegetation being smaller. This could account for the minimum humidity and minimum temperature being significantly higher in the non burnt edge. However correlation analysis showed that only the maximum temperature was correlated to vegetation distance and not minimum temperature and humidity.

The data show although there are structural differences between the two forest edges these differences only correlate with maximum temperature which was not significantly different between the two edges. The % cover of vegetation types only varied in term of dead wood cover in the upper canopy, but with no other variations. Dead wood is again not an associated habitat of the Calyptrate sub order, so its lack of presence within the high canopy should not impact the overall abundance of the three families highlighted here. Therefore with the data available for analysis the only conclusion that can be drawn is that

the burning of the adjacent savannah directly decreases the abundance of Muscidae, Calliphoridae and Tachinidae within the margins of the burnt edge forest and increases them within the burnt savannah itself. Whether the families disperse directly from the forest edge into the savannah is not clear and would require further taxonomic verification not available to this project.

Given these structural and environmental differences can we therefore conclude that the difference seen between these forest edges are a direct effect of the savannah treatment perhaps the history of the two edges. The non burnt edge was adjacent to an isolated savannah patch, previously used as farmland, before the local residents were relocated to the Gashaka enclave. The savannah itself had not been subject to a burning event for up to four years prior to this data collection. Whereas the savannah subjected to burning for this experiment was burned almost annually due to its close proximity to the historic footpath mentioned in the introduction. Successive burning events could have thinned the ground canopy sufficiently for these environmental and structural parameters to have changed significantly over time. However no records were available on the regularity or timing of the burn to this site in preceding years.

As stated previously anthropogenic burning within National Parks is illegal in Nigeria, so why does it still happen? First and foremost the enforcement capabilities of the National Park Rangers are not up to western standards, with little or no resources available to prevent such events. The National Park Rangers have to prioritise their resources, and in the case of Gashaka Gumti prevention of poaching and cattle grazing is a far higher priority. Secondly, a majority of the National Park Rangers are from the local area, either within the village enclaves themselves or population centres adjacent to the park boundary; and therefore are more likely to believe that burning is beneficial and therefore more likely not to report such events to higher authorities.

In conclusion the data are showing that burning of the adjacent savannah does have a significant effect on the abundance of some dipteran families within the Kwano Forest boundary. However as this is really the first study to specifically target the effect of burning adjacent savannah on invertebrates within the forest boundary, these results warrant further investigation. Due to time constraints it was not possible to collect samples pre and post burn within the same edge site; however this could indicate the exact effects that the burn is having on the abundance of Diptera. Collecting samples during the burn within the boundary of the forest would also potentially show if Diptera were dispersing from the savannah into the forest (although care would need to be taken to make sure that the traps themselves were not burnt).

Chapter 6: The influence of edge effects and environmental gradients on Diptera populations within the forest boundary

6.1 Introduction

Fragmentation of forest habitats is a problem that is seen all over the world, and has far reaching consequences not only for the organisms that live within the forest boundary but also for the human populations that depend on the ecological services that the forest provides. The process of forest fragmentation leads to an increase in edge effects, due to decreasing fragment size and irregularity of fragment shape, meaning that the ratio to the interior of the forest reduces to its edge (Ries et al., 2004, Chiarello, 2003). The edge can affect both the physical structure of the forest and its abiotic characteristics, such as humidity, temperature, light penetration and the influence of prevailing winds (Bierregaard et al., 1992, Laurance et al., 2002). There is also a distinct rise in tree mortality at the edge, which increases the presence of canopy gaps and therefore will increase the amount of secondary succession within the vicinity of the edge and protruding into the interior of the forest (Marsh, 2003, Laurance et al., 2002).

These ecological, environmental and physical effects will influence the abundance, diversity and community structure of the invertebrates within the forest boundary, causing increases in generalist species and decreases in forest specialists within the influence of the forest edge (Didham, 1997). Although there are certain resources that need to be present within a habitat in order for an invertebrate to survive, it is the variations in microclimate that impose the most significant effects on invertebrate populations (Foggo et al., 2001, Deans et al., 2005, Schowalter and Zhang, 2005, Ostman et al., 2009).

In Chapter 3 the use of a set of linear and non linear regression models were introduced to investigate possible edge effects present within the study site. The ordinal results showed that there were detectable edge effects within the forest in terms of dipteran abundance, environmental parameters and forest structure. Most notable was the effect of distance from the edge on the environmental parameters with minimum temperature, minimum humidity and maximum humidity (dry season only) all showing a strong relationship with distance from the edge. All three parameters had a positive relationship with the edge, meaning that minimum temperature (night temperature) is higher in the interior than at the edge and that humidity is higher within the forest interior than at the edge. Although not significant (within the linear regression analysis) there is a negative trend in correlation between maximum temperature and distance, meaning that daytime temperature tends to be lower towards the core of the forest than at the edge. These observations follow much of the research that has been previously conducted on this topic (Laurance et al., 2002, Bierregaard et al., 1992).

The influence of environmental factors on invertebrate abundance has been highlighted in the past (see Feldmeyer et al. (2008), as temperature and humidity play an important role in determining the timing of emergence, breeding and feeding resources. Chapter 4 discussed how the final dipteran generation of the season will overwinter as larvae, protected from the harsh elements, until environmental conditions are compatible with their physiology and reproductive strategy (Cecidomyiidae) (Tokuda et al., 2006). The presence of a narrow set of environmental conditions and the effect that changes within that range have on sex ratios was also discussed (Ceratopogonidae) (Bishop et al., 1996). Both these examples show the importance of the surrounding environment, but are only two of many examples that can be found in the literature (Gillespie et al., 2000, Feldmeyer et al., 2008, Tokuda et al., 2006, Bishop et al., 1996)

Therefore as the environment has such a significant effect on the abundance and life history of these invertebrates, an investigation of the nature of the relationship and the possibility of these factors being used to help predict patterns of abundance in certain dipteran families is the next logical progression. Use of the set of regression models (see Chapter 3) is the most appropriate in this case. Multiple regression models using environmental parameters would prove messy at best as the cross correlation between factors such as temperature and humidity makes the analysis complicated; therefore as well as using the distance from the edge, an independent factor for uncovering edge effect, the use of environmental parameters as a gradient of edge effects will also be discussed in this chapter.

As was discussed in Chapter 3 it is not necessary to detect the exact nature of the relationship, rather to find the most suitable model and then use the parameters of each equation to extract further information about the relationship and the effect that is being investigated. Investigation of these regression models showed that the higher level models such as the logarithmic and unimodal models fit data better when there were positive and negative independent distance values. This means that they analyse the relationship between the independent and dependent factors across the boundary of the forest, rather than just the internal forest effects. Linear regression has this property but as was shown does not always support the models as well as the logarithmic and unimodal curves. The power model was successful at detecting relationships within the boundary but cannot support negative independent values. The power model will be useful in this chapter as environmental parameters will be investigated as independent factors and therefore will have no negative values for the two higher models (logarithmic and unimodal) to fit curves to.

This chapter will further investigate edge effects and the use of this set of models. However in this chapter edge effects on individual families of Diptera will be explored at different levels in the canopy. As in the previous chapter the influence of the edge on seasonal changes and at differing heights will be studied, in addition to this environmental gradients will be used in the place of spatial gradients. Data will also be split between edge treatments in order to study the effects of burning at the edge of the forest on Diptera present within the habitat.

6.2 Methodology

Detailed methodology concerning the linear and non linear models suggested by Ewers & Didham (2006) and Shaw et al (2007) used in this chapter was outlined in Chapter 3 and will not be repeated here. However in addition to this a more detailed look at correlations between family level abundance and spatial and environmental gradients will also be discussed. Fourteen families, suborders and taxanomic groups were initially analysed, and where the data were suitable further more detailed analysis was performed. The families, taxanomic groups and suborders included in the analysis were; Ceratopogonidae, Sciaridae, Mycetophilidae, Chironomidae, Cecidomyioidae, Phoridae, Sarcophagidae, Tachinidae, Muscidae, and Calliphoridae (families), and Acalyptrate, Nematocera, Brachycera and Calyptrate. All family, group and suborder abundance data were tested for normality with a Kolmogorov-Smirnov test, no family or suborder data set proved to have a normal distribution, therefore all were transformed using a $\log_{10}(x+2)$ transformation. A +2 was added to the transformation as later analysis (power model) does not allow for zeros within the dependent factor, so using a +1 addition to the transformation would still leave zero results and the logarithmic regression unusable. Therefore using a +2 addition to the transformation means that no further transformations would be needed for higher

level analysis. Spearman's correlations of family, group and suborder abundance against distance and environmental parameters were performed, Spearman's correlations were preferred to Pearson's correlations not only because the data may not have been normally distributed but because this analysis is investigating both linear and non linear relationships within the data and the Spearman's correlation allows for this difference. Further to this where data were normally distributed a further linear regression test was performed. Residuals were analysed to confirm that regression assumptions were not violated through a Kolmogorov-Smirnov test for normality, mean of zero and the residuals were plotted against the independent factor to make sure that there were no patterns present.

The data were first split between periods of rain and no rain and then by height category (ground, mid and high canopy). As before the savannah data was added to each of the data sets to explore the effect across the forest boundary (with the exception of the power model, see above). Edge treatment was then introduced. Internal data were added to both burnt and non burnt data sets so that the full range of distances could be included in the analysis. Year 2 environmental data were split between burnt and non burnt edges (each treatment again included internal data). As the environmental data includes the effects of seasonal change within the data there was no need to split the data sets between periods of rain and no rain.

6.3 Results

6.3.1 The effect of distance from edge and height within the canopy on family, group and suborder dipteran abundance

Initially data were split between periods of rain and no rain and a Spearmans correlation performed on all non transformed family, group and suborder abundances. Table 6.1 below shows these results. Families, group and suborders were correlated to distance from the edge.

Table 6.1, Spearmans Correlations of family, group and suborder abundance to distance from the edge

Family/Group/Suborder	Season	Height	r_s
Ceratopogonidae	Dry		0.076
	Wet		-0.099
	Dry	Ground	0.058
		Mid	0.340*
		High	0.124
	Wet	Ground	-0.507**
		Mid	0.282
		High	0.032
Sciaridae	Dry		0.211*
	Wet		0.138
	Dry	Ground	0.145
		Mid	0.200
		High	0.302

	Wet	Ground	-0.155
		Mid	0.293*
		High	0.314*
Mycetophilidae	Dry		0.279**
	Wet		-0.042
	Dry	Ground	0.211
		Mid	0.261
		High	0.432**
	Wet	Ground	-0.105
		Mid	0.082
		High	0.152
Chironomidae	Dry		0.16
	Wet		0.217**
	Dry	Ground	0.142
		Mid	0.161
		High	0.294
	Wet	Ground	-0.027
		Mid	0.155
		High	0.455**
Cecidomyiidae	Dry		-0.179*
	Wet		0.076
	Dry	Ground	-0.331*
		Mid	0.237
		High	0.359*
	Wet	Ground	0.039
		Mid	0.127

		High	0.047
Total Nematocera	Dry		0.027
	Wet		0.175*
	Dry	Ground	-0.255*
		Mid	0.446**
		High	0.537**
	Wet	Ground	-0.100
		Mid	0.279
		High	0.309*
Total Acalyptrate	Dry		-0.272**
	Wet		0.273**
	Dry	Ground	-0.378**
		Mid	0.096
		High	0.135
	Wet	Ground	0.028
		Mid	0.471**
		High	0.285
Phoridae	Dry		0.123
	Wet		0.177*
	Dry	Ground	0.199
		Mid	0.024
		High	0.351*
	Wet	Ground	-0.044
		Mid	0.255
		High	0.282
Total Brachycera	Dry		0.092
	Wet		0.102

	Dry	Ground	0.155
		Mid	0.173
		High	0.369*
	Wet	Ground	-0.188
		Mid	0.285
		High	0.172
Sarcophagidae	Dry		-0.213*
	Wet		-0.177
	Dry	Ground	-0.366**
		Mid	0.267
		High	-0.244
	Wet	Ground	-0.208
		Mid	0.000
		High	0.029
Muscidae	Dry		-0.413**
	Wet		-0.238**
	Dry	Ground	-0.517**
		Mid	0.047
		High	0.005
	Wet	Ground	-0.422**
		Mid	-0.020
		High	0.017
Tachinidae	Dry		-0.158
	Wet		0.055
	Dry	Ground	-0.221
		Mid	0.186

		High	0.064
	Wet	Ground	0.073
		Mid	0.017
		High	-0.046
Calliphoridae	Dry		-0.108
	Wet		-0.047
	Dry	Ground	-0.136
		Mid	0.047
		High	-0.143
	Wet	Ground	-0.234
		Mid	0.120
		High	0.000
Total Calyptrate	Dry		-0.349**
	Wet		-0.125
	Dry	Ground	-0.538**
		Mid	0.320*
		High	-0.171
	Wet	Ground	-0.399**
		Mid	0.113
		High	0.008

* significant to the 0.05 level

** Significant to the 0.005 level

The results from the wet and dry season show a mix of significant and non significant associations between the relative dipteran family,group and suborder abundances and the distance from the edge. The Calyptrate abundances show a negative association, Nematocera abundance a positive and Acalyptrate changing from positive to negative between wet and dry season. Once the data were split between height categories the results

are quite different. There is still the general trend of positive and negative associations however we see, for example in the total Nematocera abundance that the dry season height categories all have a significant association with edge, especially in the mid and high canopy. Whereas when height was not taken into account there was no association. The nature of the Spearman's correlation means that these results don't necessarily point to a linear relationship but to a monotonic trend, sharing continued gradual/incremental changes with distance from the edge.

As all these data sets were not normally distributed all were transformed and retested for normality using a Kolmogorov-Smirnov test. Only transformed Cecidomyiidae and Total Nematocera abundance had normal distribution, so could be taken to the next level of analysis.

The Spearman's edge effect correlations for Cecidomyiidae and total Nematocera abundance and distance from the edge were weak but significant therefore a linear regression was performed to establish if there was indeed a significant linear relationship. Prior to analysis outliers were identified and removed so as to keep regression assumptions from being violated. Neither Cecidomyiidae, $r^2 = 0.001$, *ns*, or total Nematocera, $r = 0.149$, $r^2 = 0.002$, *ns*, showed a significant linear relationship in during the dry season or the wet season, $r^2 = 0.00$, *ns*, and $r^2 = 0.024$, *ns*, respectively. Dry season mid and high canopy Nematocera abundance did show a significant linear relationship, $r^2 = 0.231$, $p < 0.005$, and $r^2 = 0.268$, $p < 0.005$, respectively. The Cecidomyidae abundance did not show any significant linear relationships at any height to the distance from the edge. The analysis did support regression assumptions and therefore both the transformed Cecidomyiidae and total Nematocera abundance data were taken forward for further investigation using non linear regression analysis.

Data were split first between wet and dry season and then the data were also explored within each of the height categories for both seasons. All analysis was conducted on the transformed abundances. As in the previous chapter starting point for the non linear function in PASW 17 were calculated from fitting data points to the equation and creating an estimate of the scaling constant (B_2). The intercept point (B_1) and asymptote (B_0) were estimated by exploring the range of values for each of the dependent data sets. Table 6.2 below shows the results of the power model analysis.

Table 6.2. Power model analysis on transformed seasonal and height category Cecidomyiidae and Nematocera abundance against distance from the edge.

Dependent	Season	Height	*B_2	*r*	r^2	$D_{1/2}$ (m)
Nematocera	Dry		0.013	0.400	0.16	53.32
	Wet		0.038	0.228	0.052	18.24
	Dry	Ground	0.013	0.356	0.127	53.31
		Mid	0.018	0.499	0.249	38.51
		High	-	-	-	-
	Wet	Ground	0.002	0.110	0.012	346.57
		Mid	0.06	0.310	0.096	11.55
		High	0.061	0.324	0.105	11.36
Cecidomyiidae	Dry		0.018	0.219	0.048	38.51
	Wet		-	-	-	-
	Dry	Ground	0.01	0.237	0.056	69.31
		Mid	0.021	0.266	0.071	33.01
		High	0.09	0.353	0.125	7.70

Wet	Ground	-	-	-	-
	Mid	0.065	0.063	0.004	10.66
	High	0.075	0.070	0.005	9.24

- Residual Assumptions not met/iteration limit reached/large standard errors

* positive scaling constant from equation

$D_{1/2}$ Midpoint of the effect

If we accept that r^2 values greater than 0.09 show a weak relationship (corresponds to a 0.31 *r* value which would usually prove significant in correlation or linear regression analysis) between the relative abundances and distance from the edge, we see that when height data are grouped there is a significant relationship during the dry season, $r = 0.400$, $r^2 = 0.16$, which gives a half distance of 53.32 m from the edge of the forest into the core. The half distance is the point on the *x* axis where the effect is at its greatest, therefore the point where the increase in Nematocera abundance is at its highest. Unfortunately the wet season results did not show a significant relationship so we cannot accept the half distance provided by the equation. However once the data are split between height categories, the mid canopy abundances in dry and wet season both show significant relationships. The half distances from wet and dry season show that the edge effect moves closer to the edge of the forest during the rains, from 38.51 m from the forest edge in the dry season to 11.55 m in the wet season. The results also show that there are distinct differences in the midpoint at different heights, with the dry season ground canopy total Nematocera abundance midpoint being much further into the forest core than the mid canopy midpoint, 53.31 m and 38.51 m respectively.

The Cecidomyiidae and Nematocera data were now assessed using the logarithmic model. As this equation allows for negative independent variables, the savannah data was added to the independent data to increase its range. Estimation of the constants for the non linear regression analysis was done by estimating the upper and lower values of the dependent

factors for constants B_0 and B_1, B_2 was shown to be the mid point of the effect in a previous chapter, therefore the mid points found using the power model were used, and the scaling constant, B_3, was set at a starting value of 0.01. As with previous model assessments if iteration limits were reached, standard errors too high or residual assumptions not met then the analysis was discounted. 1^{st} and second derivatives were calculated and graphed to ascertain the magnitude and extent of the effects within the models. Table 6.3, below, show the results of this regression analysis.

Table 6.3. Logarithmic regression model results.

Dependent	Season	Height	r	r^2	Midpoint (m)	Magnitude	Extent (m)
Nematocera	Dry		-	-	-	-	-
	Wet		0.176	0.031	126.70	-0.248	39 – 214.5
	Dry	Ground	-	-	-	-	-
		Mid	0.520	0.270	61.49	0.62	27-96
		High	-	-	-	-	-
	Wet	Ground	-	-	-	-	-
		Mid	0.587	0.344	23.45	0.362	*
		High	-	-	-	-	-
Cecidomyiidae	Dry		-	-	-	-	-
	Wet		-	-	-	-	-
	Dry	Ground	-	-	-	-	-
		Mid	0.331	0.110	64.45	0.118	38 - 91
		High	0.4	0.160	7.45	0.605	-3 – 18.5
	Wet	Ground	-	-	-	-	-
		Mid	-	-	-	-	-
		High	-	-	-	-	-

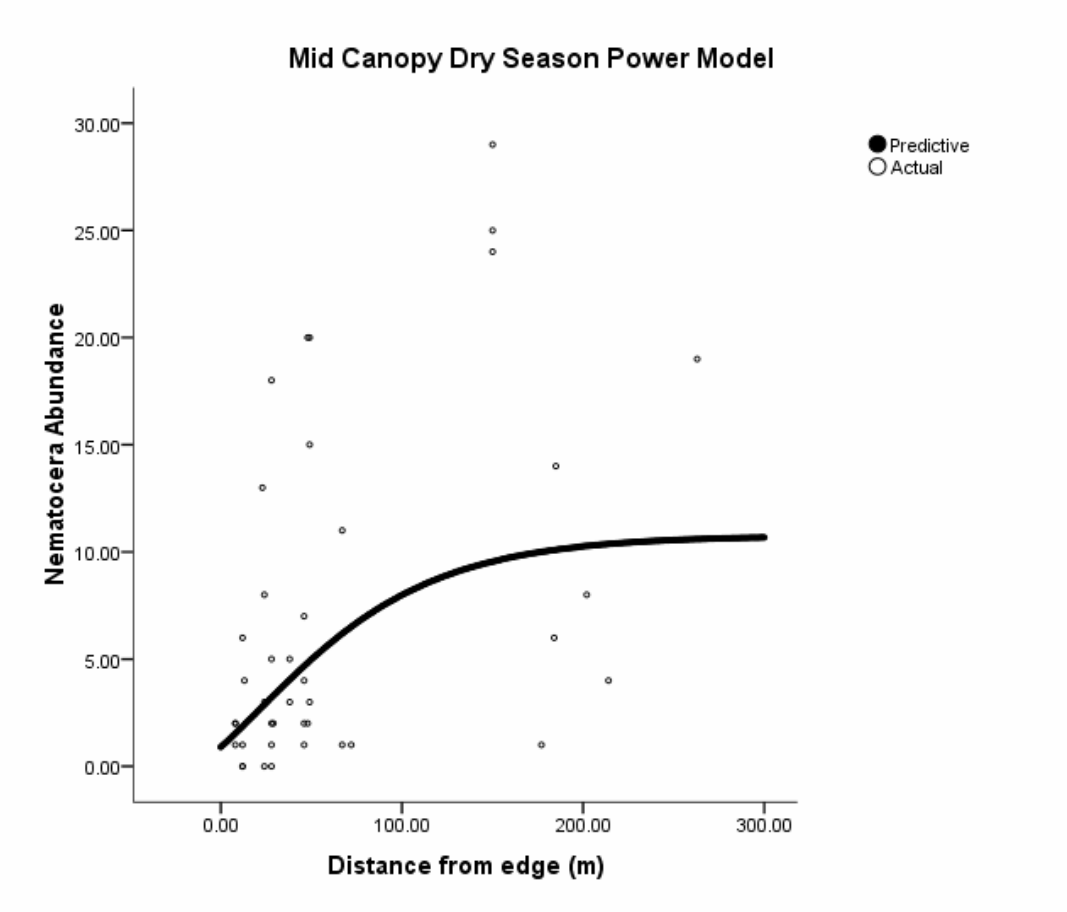
Midpoint calculated from B_2, magnitude from 1st derivatives and extent from 2nd derivatives

- Residual assumptions not met/iteration limit reached/large standard errors

* Derivatives reached exponential limit and could not be plotted

Fitting the logarithmic model was not very successful, only five out of 16 data groups showed a logarithmic relationship. Of those we can however see a strong relationship between dry and wet season mid canopy Nematocera abundance and the distance from the

edge, $r = 0.520$, $r^2 = 0.27$, and $r = 0.587$, $r^2 = 0.344$ respectively. However we also saw a similarly strong relationship with the dry season mid canopy power model. The two model curves are potted in fig 6.1, below, to show the differences between the two plots.



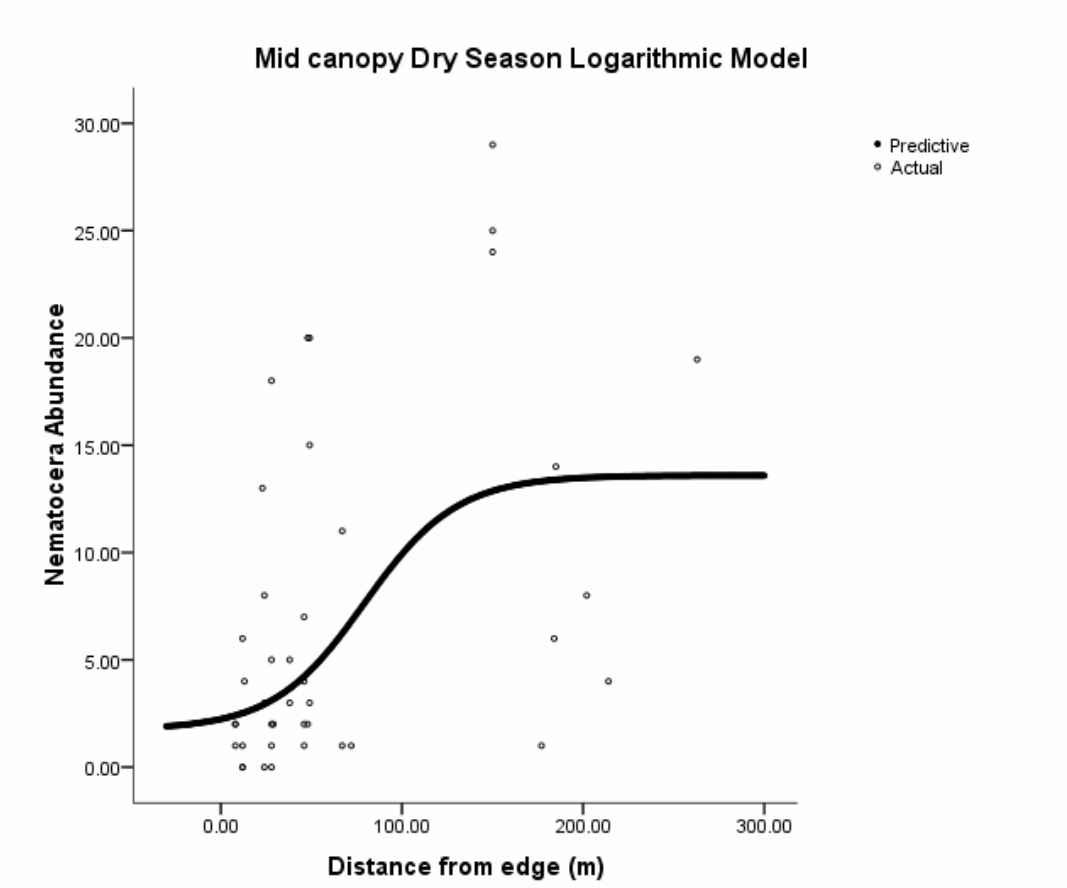


Fig 6.1. Predicted and measured dry season mid canopy Nematocera abundances (per trap day) from power and logarithmic analysis. Note: an outlier was removed when creating these graphs as its presence made the relationship less clear).

When trying to fit the unimodal model, no combination of starting points were able to achieve a result that did not violate either the residual assumptions, have a large standard error in one or more of the constants, or the iteration limit was reached within the analysis. Therefore all unimodal results were discounted and will not be shown here.

Finally, as in the previous chapter all models were compared using AIC weights, each calculated from the residual sum of squares from each of the regression model fits. These results are displayed in table 6.4, below.

Table 6.4. AIC weights for all linear and non linear models completed for this analysis

Dependent	Season	Height	Model	RSS	*AIC_c	Δ_i	w_i
Total	Dry		Linear	17.532	-269.4	0	0.999
Nematocera			Power	11.632	-245.3	24.08	5.8E-6
Abundance			Log	-	-	-	-
			Uni	-	-	-	-
	Wet		Linear	19.298	-295.3	0	0.926
			Power	17.762	-265.5	29.84	3.07E-7
			Log	20.204	-290.3	5.04	0.074
			Uni	-	-	-	-
	Dry	Ground	Linear	5.751	-140.7	0	1
			Power	2.533	-82.6	2.4E-13	2.4E-13
			Log	-	-	-	-
			Uni	-	-	-	-
		Mid	Linear	4.958	-83.108	1.967	0.255
			Power	3.794	-85.075	0	0.683
			Log	4.704	-80.282	4.793	0.062
			Uni	-	-	-	-
		High	Linear	4.087	-81.289	0	1
			Power	-	-	-	-
			Log	-	-	-	-
			Uni	-	-	-	-
	Wet	Ground	Linear	7.872	-112.4	0	0.868
			Power	5.336	-83.8	28.601	5.3E-07
			Log	7.748	-108.6	3.759	0.132
			Uni	-	-	-	-

		Mid	Linear	6.729	-81.850	70.628	4.6E-16
			Power	6.393	-81.803	70.676	4.5E-16
			Log	1.302	-152.47	0	1
			Uni	-	-	-	-
		High	Linear	5.324	-89.464	0.474	0.441
			Power	4.993	-89.938	0	0.559
			Log	-	-	-	-
			Uni	-	-	-	-
Cecidomyiidae	Dry		Linear	16.178	-286.50	0	0.999
Abundance			Power	10.986	-255.01	31.490	1.5E-07
			Log	-	-	-	-
			Uni	-	-	-	-
	Wet		Linear	14.714	-325.58	0	1
			Power	-	-	-	-
			Log	-	-	-	-
			Uni	-	-	-	-
	Dry	Ground	Linear	5.657	-135.25	0	1
			Power	2.514	-82.838	52.420	4.1E-12
			Log	-	-	-	-
			Uni	-	-	-	-
		Mid	Linear	4.811	-84.373	2.925	0.184
			Power	3.589	-87.297	0	0.794
			Log	4.715	-80.184	7.113	0.023
			Uni	-	-	-	-

	High	Linear	2.74	-96.883	0	0.635
		Power	2.528	-93.774	3.109	0.134
		Log	2.53	-94.860	2.023	0.231
		Uni	-	-	-	-
Wet	Ground	Linear	5.214	-136.7	0	1
		Power	-	-	-	-
		Log	-	-	-	-
		Uni	-	-	-	-
	Mid	Linear	6.888	-80.776	1.168	0.358
		Power	5.181	-81.944	0	0.642
		Log	-	-	-	-
		Uni	-	-	-	-
	High	Linear	5.255	-90.051	0	0.756
		Power	5.237	-87.791	2.260	0.244
		Log	-	-	-	-
		Uni	-	-	-	-

- Residual assumptions not met/iteration limit reached/large standard errors

* Corrected AIC used as n/K < 40

Of the two significant linear relationships, dry season mid and high canopy Nematocera abundance, their corresponding AIC weights confirm that they are an acceptable model for this analysis. However in the case of the mid canopy results we see that the power model is in fact a better model, with a much higher AIC weight. The logarithmic model was only acceptable in mid canopy wet season Nematocera abundance, meaning that there could be a shift in relationship between the two seasons. When the height categories are grouped together for the Cecidomyiidae abundance the AIC weights show that the linear model is the most acceptable and therefore we can say that there is no detectable relationship using

this set of models. However once the data were split between height categories the power model becomes as acceptable as the linear. However as there was only one weak power relationship in the dry season high canopy results and that the logarithmic relationship was in fact slightly stronger (r^2 = 0.160 vs r^2 = 0.125) than the power model, acceptance of the power model for Cecidomyiidae would not be the right choice.

6.3.2 The effect of distance from edge and treatment on family, group and suborder dipteran abundance

Still using distance from the edge of the forest as an independent factor, the data were now split between wet and dry periods and then by edge treatment (burnt and non burnt). As with the previous analysis the untransformed data was first explored using Spearman's correlations to look for underlying trends in the association between distance, treatment and Diptera abundance shown in table 6.5, below.

Table 6.5. Spearman's correlations of Diptera families abundance (per trap day) grouped by treatment against distance from the edge

Family/Group/Suborder	Season	Treatment	r_s
Ceratopogonidae		Burnt	0.123
		Non Burnt	0.056
	Dry	Burnt	0.172
		Non Burnt	0.129
	Wet	Burnt	-0.012
		Non Burnt	-0.172
Sciaridae		Burnt	0.345**
		Non Burnt	0.235**

	Dry	Burnt	0.316**
		Non Burnt	0.231*
	Wet	Burnt	0.284**
		Non Burnt	0.092
Mycetophilidae		Burnt	0.177*
		Non Burnt	0.113
	Dry	Burnt	0.302**
		Non Burnt	0.301**
	Wet	Burnt	0.054
		Non Burnt	-0.081
Chironomidae		Burnt	0.282**
		Non Burnt	0.226**
	Dry	Burnt	0.255*
		Non Burnt	0.080
	Wet	Burnt	0.234*
		Non Burnt	0.194
Cecidomyiidae		Burnt	0.076
		Non Burnt	-0.05
	Dry	Burnt	0.062
		Non Burnt	-0.25*
	Wet	Burnt	0.067
		Non Burnt	0.073
Total Nematocera		Burnt	0.076
		Non Burnt	0.09
	Dry	Burnt	0.267*
		Non Burnt	-0.076

	Wet	Burnt	0.233*
		Non Burnt	0.133
Total Acalyptrate		Burnt	0.314**
		Non Burnt	0.137**
	Dry	Burnt	0.264*
		Non Burnt	0.044
	Wet	Burnt	0.323**
		Non Burnt	0.289**
Phoridae		Burnt	0.203*
		Non Burnt	0.107
	Dry	Burnt	0.203
		Non Burnt	0.119
	Wet	Burnt	0.237*
		Non Burnt	0.153
Total Brachycera		Burnt	0.177*
		Non Burnt	0.036
	Dry	Burnt	0.238*
		Non Burnt	0.052
	Wet	Burnt	0.0165
		Non Burnt	0.093
Sarcophagidae		Burnt	-0.218**
		Non Burnt	-0.217**
	Dry	Burnt	-0.244*
		Non Burnt	-0.092
	Wet	Burnt	-0.022
		Non Burnt	-0.223*

Muscidae		Burnt	-0.323**
		Non Burnt	-0.437**
	Dry	Burnt	-0.330**
		Non Burnt	-0.504**
	Wet	Burnt	-0.278**
		Non Burnt	-0.237*
Tachinidae		Burnt	-0.029
		Non Burnt	-0.178*
	Dry	Burnt	-0.057
		Non Burnt	-0.218
	Wet	Burnt	-0.056
		Non Burnt	-0.022
Calliphoridae		Burnt	-0.162*
		Non Burnt	-0.111
	Dry	Burnt	-0.186
		Non Burnt	-0.127
	Wet	Burnt	-0.104
		Non Burnt	0.036
Total Calyptrate		Burnt	-0.211**
		Non Burnt	-0.376**
	Dry	Burnt	-0.248*
		Non Burnt	-0.407**
	Wet	Burnt	-0.098
		Non Burnt	-0.241*

* significant to the 0.05 level

** Significant to the 0.005 level

The Ceratopogonidae showed no significant association at either the burnt or non burnt edge during either of the seasonal phases. The Cecidomyiidae, Nematocera, Phoridae, Brachycera, Tachinidae and Calliphoridae only showed one or two weak associations with distance from the edge. Where as all other family, group and suborder abundances showed stronger significant associations with the distance from the edge for both edge treatments and in both wet and dry season. Sarcophagidae, Muscidae and total Calyptrate abundances were all negatively associated, where as Sciaridae, Mycetophilidae, Chironomidae and total Acalyptrate were all positively associated with the distance from the edge in both seasons and at each of the treatment edges.

All data sets were tested for normality with a Kolmogorov-Smirnov test, and again only the Cecidomyiidae and Nematocera abundances showed a normal distribution. Therefore only these two groups were taken forward to the higher level analysis. In the first instance a linear regression was performed on the transformed data sets to look for any significant relationships present within the data. The Cecidomyiidae abundance data showed no significant relationships between burnt or non burnt edges and distance from the edge of the forest, and there was no significant relationship shown when season was taken into account. However the transformed Nematocera Abundance did show some significant relationships which are shown in table 6.6, below. Residual assumptions were analysed to make sure that all results could be accepted.

Table 6.6, Linear Regression analysis for transformed total Nematocera abundance (per trap day) using distance from the edge of the habitat as the independent variable.

Dependent	Season	Treatment	*r*	r^2
Total		Burn	0.324	0.105**
Nematocera		No Burn	0.155	0.024*
	Dry	Burn	0.342	0.177**
		No Burn	0.104	0.011
	Wet	Burn	0.241	0.058*
		No Burn	0.111	0.012

* significant to the 0.05 level

** Significant to the 0.005 level

Both groups of data were taken to the next level of analysis. The starting point for all the constants was estimated as above and data were split as for the linear regression analysis. The results of the power model are displayed in the table 6.7, below. As before the midpoint of the effect is calculated from the constant B_2.

Table6.7. Power model analysis on transformed seasonal and treatment category Cecidomyiidae and Nematocera abundance (per trap day) against distance from the edge.

Dependent	Treatment	Season	*B_2	*r*	r^2	$D_{1/2}$ (m)
Nematocera	Burnt		0.021	0.432	0.187	33.01
	Non Burnt		0.005	0.286	0.082	138.63
	Burnt	Dry	0.019	0.539	0.290	36.48
		Wet	0.300	0.300	0.090	2.31
	Non Burnt	Dry	0.007	0.394	0.156	99.02
		Wet	-	-	-	-

Cecidomyiidae	Burnt		0.038	0.205	0.042	18.24
	Non Burnt		0.009	0.148	0.022	77.02
	Burnt	Dry	0.033	0.319	0.102	21.00
		Wet	0.038	0.084	0.007	18.24
	Non Bunrt	Dry	0.002	0.230	0.053	346.57
		Wet	0.107	0.077	0.006	6.49

- Residual Assumptions not met/iteration limit reached/large standard errors

* positive scaling constant from equation

$D_{1/2}$ Midpoint of the effect

Both burnt and non burnt dry season and grouped burnt data all showed acceptable power relationships with the distance from the edge for the Nematocera abundance. The Cecidomyiidae abundance results only showed an acceptable relationship in the dry season non burnt data.

The logarithmic model was now fitted to the data, constants were estimated for the non linear function in PASW 17 as above and attention was paid to residual assumptions, iteration limits and standard errors of the calculated constants. The results of the logarithmic model fit are seen in table 6.8, below. As before savannah data was added to the data set as the logarithmic model assumes the dataset to have positive and negative independent values.

Table 6.8. Logarithmic regression model results.

Dependent	Treatment	Season	r	r^2	Midpoint (m)	Magnitude	Extent (m)
Transformed	Burnt		0.345	0.119	60.62	-0.299	43 – 78
Nematocera	Non Burnt		-	-	-	-	-
Abundance	Burnt	Dry	0.394	0.155	79.75	-0.34	63 - 96
		Wet	-	-	-	-	-
	Non Burnt	Dry	-	-	-	-	-
		Wet	-	-	-	-	-
Transformed	Burnt		-	-	-	-	-
Cecidomyiidae	Non Burnt		-	-	-	-	-
Abundance	Burnt	Dry	-	-	-	-	-
		Wet	-	-	-	-	-
	Non Burnt	Dry	-	-	-	-	-
		Wet	-	-	-	-	-

Midpoint calculated from B_2, magnitude from 1st derivatives and extent from 2nd derivatives

- Residual assumptions not met/iteration limit reached/large standard errors

Here again we see that the logarithmic model fails to fit a large proportion of the analysis. Only two data sets (that of the grouped burnt edge and the dry season burnt edge Nematocera abundance) were stable enough for publication, the power model was the better fitting model out of these higher level regression equations.

As with the previous section the unimodel regression failed to fit the data, with iteration limits being met, standard errors too high or residual assumptions not being met. Therefore the results will not be displayed here.

As in the previous section the successful model fits were analysed using AIC weights, displayed below in table 6.9. Only models that id not violate one or more of the assumptions were analysed.

Table 6.9. AIC calculations for all plausible models.

Dependent	Treatment	Season	Model	RSS	*AIC_c	Δ_i	w_i
Total	Burn		Linear	24.990	-352.35	0	0.666
Nematocera			Power	21.503	-334.07	18.178	7.5E-05
Abundance			Log	24.603	-350.87	1.382	0.334
			Uni	-	-	-	-
	No Burn		Linear	31.198	-337.14	0	1
			Power	26.858	-294.11	43.030	4.5E-10
			Log	-	-	-	-
			Uni	-	-	-	-
	Burnt	Dry	Linear	10.759	-157.20	0	0.390
			Power	7.547	-157.07	0.123	0.365
			Log	10.297	-156.27	0.933	0.244
			Uni	-	-	-	-
		Wet	Linear	13.29	-195.57	0	0.999
			Power	12.542	-180.89	14..679	0.001
			Log	-	-	-	-
			Uni	-	-	-	-
	No Burn	Dry	Linear	14.209	-148.55	0	0.999
			Power	9.579	-130.61	17.939	0.001
			Log	-	-	-	-
			Uni	-	-	-	-

		Wet	Linear	16.177	-197.28	0	1
			Power	-	-	-	-
			Log	-	-	-	-
			Uni	-	-	-	-
Total Cecidomyiidae Abundance	Burn		Linear	21.587	-378.74	0	1
			Power	19.161	-353.33	25.416	3.0E-06
			Log	-	-	-	-
			Uni	-	-	-	-
	No Burn		Linear	27.173	-363.38	0	1
			Power	22.406	-324.19	39.190	3.1E-09
			Log	-	-	-	-
			Uni	-	-	-	-
	Burnt	Dry	Linear	10.297	-160.76	0	0.932
			Power	7.708	-155.53	5.220	0.068
			Log	-	-	-	-
			Uni	-	-	-	-
		Wet	Linear	11.230	-212.41	0	1
			Power	11.025	-193.01	19.403	6.1E-05
			Log	-	-	-	-
			Uni	-	-	-	-
	No Burn	Dry	Linear	13.111	-155.76	0	1
			Power	8.511	-139.50	16.580	2.5E-04
			Log	-	-	-	-
			Uni	-	-	-	-

Wet	Linear	13.93	-202.87	0	1
	Power	13.51	-179.79	23.072	9.8E-06
	Log	-	-	-	-
	Uni	-	-	-	-

- Residual assumptions not met/iteration limit reached/large standard errors

* Corrected AIC used as n/K < 40

The Cecidomyidae abundance data show that the linear model is the best model to use on that particular data. The power model did not score well with the AIC weighting system, with all cases being less than 10% of the linear (see Chapter 3). The Nematocera Abundance data sets are more of a mixed bag, but in all cases the linear model performed well within the family of models used. Only in the dry season burnt edge can we accept the power and logarithmic models as accurately predicting the relationship between the Nematocera abundance and distance from the edge.

6.3.3 The relationship between environmental gradients and the effects of treatment on family, group and suborder dipteran abundance

Previous sections of this chapter and the preliminary results chapter investigated spatial gradients as a basis for detecting and investigating underlying edge effects adjacent to the forest boundary. In this section environmental gradients will be used in the place of distance from the edge to study seasonal shifts in abundance. Maximum and minimum temperature and maximum and minimum humidity were used as independent factors with the various dipteran families, group and suborder data used as dependent data. Family, group and suborder data were split between treatment groups (burn and no burn) with the

internal data set added, so that the burn data consisted of burn and internal and the non burnt data consisted of non burnt and internal data.

Initially all 14 suborder, group and family abundances were explored with a Spearman's correlation to investigate any underlying relationships between the four environmental parameters and the abundance of Diptera. The results are shown in table 6.10, below. Using the environmental parameters as a gradient meant that there was no need to split the data between periods of rain and no rain as the data set would intrinsically build that into the analysis.

Table 6.10. Spearman's correlations of dipteran abundance (per trap day) environmental parameters, data split by edge treatment

Family/Group/ Suborder Abundance	Environmental Parameter	Treatment	r_s
Total Acalyptrate	Min Temp		0.066
		Burn	0.104
		No Burn	-0.069
	Max Temp		0.073
		Burn	-0.011
		No Burn	0.146
	Min Humidity		0.052
		Burn	0.128
		No Burn	-0.065
	Max Humidity		0.252**
		Burn	0.330**
		No Burn	0.184

Ceratopogonidae	Min Temp		0.102
		Burn	0.184
		No Burn	-0.077
	Max Temp		-0.230*
		Burn	-0.179
		No Burn	-0.142
	Min Humidity		0.371**
		Burn	0.334**
		No Burn	0.272*
	Max Humidity		0.374**
		Burn	0.362**
		No Burn	0.297**
Sciaridae	Min Temp		0.149
		Burn	0.249*
		No Burn	0.046
	Max Temp		-0.185*
		Burn	-0.102
		No Burn	-0.035
	Min Humidity		0.278**
		Burn	0.220*
		No Burn	0.140
	Max Humidity		0.462**
		Burn	0.431**
		No Burn	0.379**
Mycetophilidae	Min Temp		0.177*
		Burn	0.264*
		No Burn	0.081

	Max Temp		-0.249**
		Burn	-0.148
		No Burn	-0.248*
	Min Humidity		0.220*
		Burn	0.107
		No Burn	0.191
	Max Humidity		0.300**
		Burn	0.266*
		No Burn	0.258*
Chironomidae	Min Temp		0.111
		Burn	0.248*
		No Burn	-0.120
	Max Temp		-0.115
		Burn	0.005
		No Burn	0.150
	Min Humidity		0.241*
		Burn	0.143
		No Burn	0.050
	Max Humidity		0.547**
		Burn	0.524**
		No Burn	0.443**
Cecidomyiidae	Min Temp		-0.050
		Burn	0.088
		No Burn	-0.188
	Max Temp		-0.263**
		Burn	-0.154
		No Burn	-0.226*

	Min Humidity		0.350**
		Burn	0.290*
		No Burn	-0.316**
	Max Humidity		0.467**
		Burn	0.447**
		No Burn	0.486**
Total Nematocera	Min Temp		0.076
		Burn	0.216*
		No Burn	-0.154
	Max Temp		-0.226*
		Burn	-0.094
		No Burn	-0.127
	Min Humidity		0.372**
		Burn	0.283*
		No Burn	0.242*
	Max Humidity		0.576**
		Burn	0.558**
		No Burn	0.523**
Phoridae	Min Temp		-0.036
		Burn	0.029
		No Burn	-0.223*
	Max Temp		0.117
		Burn	0.169
		No Burn	0.221*
	Min Humidity		0.068
		Burn	0.073
		No Burn	-0.031

	Max Humidity		0.278**
		Burn	0.335**
		No Burn	0.216*
Total Brachycera	Min Temp		-0.009
		Burn	0.042
		No Burn	-0.191
	Max Temp		0.079
		Burn	0.186
		No Burn	0.129
	Min Humidity		0.104
		Burn	0.057
		No Burn	0.051
	Max Humidity		0.307**
		Burn	0.352**
		No Burn	0.267*
Sarcophagidae	Min Temp		-0.160
		Burn	-0.063
		No Burn	-0.249*
	Max Temp		0.187*
		Burn	0.060
		No Burn	0.229*
	Min Humidity		-0.198*
		Burn	-0.083
		No Burn	-0.258*
	Max Humidity		-0.270**
		Burn	-0.164
		No Burn	-0.369**

Muscidae	Min Temp		-0.129
		Burn	-0.176
		No Burn	-0.070
	Max Temp		0.111
		Burn	0.016
		No Burn	0.145
	Min Humidity		-0.113
		Burn	-0.016
		No Burn	-0.197
	Max Humidity		-0.043
		Burn	-0.075
		No Burn	-0.085
Tachinidae	Min Temp		-0.013
		Burn	0.026
		No Burn	-0.136
	Max Temp		0.055
		Burn	0.050
		No Burn	0.103
	Min Humidity		-0.038
		Burn	-0.035
		No Burn	0.103
	Max Humidity		0.070
		Burn	0.094
		No Burn	-0.25
Calliphoridae	Min Temp		-0.072
		Burn	-0.120
		No Burn	-0.150

	Max Temp		0.085
		Burn	0.190
		No Burn	0.110
	Min Humidity		-0.004
		Burn	-0.062
		No Burn	-0.036
	Max Humidity		0.098
		Burn	0.089
		No Burn	0.09
Total Calyptrate	Min Temp		-0.115
		Burn	-0.124
		No Burn	-0.228*
	Max Temp		0.153
		Burn	0.076
		No Burn	0.239*
	Min Humidity		-0.121
		Burn	-0.050
		No Burn	-0.248*
	Max Humidity		-0.040
		Burn	0.006
		No Burn	-0.159

* significant to the 0.05 level

** Significant to the 0.005 level

All family, group and suborder abundance showed a significant association with maximum humidity, with the exception of the Calyptrates. Minimum humidity also showed some association with Ceratopogonidae and total Nematocera. Although there were a few

significant temperature correlations, the number was commensurate with the overall null hypothesis of randomness.

When tested for normality using a Kolmogorov-Smirnov test only the transformed Cecidomyiidae and total Nematocera abundances were normally distributed so only they were taken forward to linear regression. The results of the linear regression analysis are displayed in table 6.11, below. As before residual assumption were checked before accepting the results given by the analysis.

Table 6.11, Linear regression of Cecidomyiidae and Total Nematocera abundances (per trap day) against minimum and maximum temperature and minimum and maximum humidity.

Dependent	Independent	Treatment	*r*	r^2
Total	Min Temp		0.128	0.016
Nematocera		Burn	0.253	0.064*
		No Burn	0.122	0.015
	Max Temp		0.164	0.028
		Burn	0.013	0
		No Burn	0.105	0.011
	Min Humidity		0.386	0.149**
		Burn	0.347	0.12**
		No Burn	0.249	0.062*
	Max Humidity		0.526	0.277**
		Burn	0.582	0.339**
		No Burn	0.417	0.174**

Cecidomyiidae	Min Temp		0.003	0
		Burn	0.137	0.019
		No Burn	0.145	0.021
	Max Temp		0.212	0.045*
		Burn	0.079	0.006
		No Burn	0.180	0.033
	Min Humidity		0.348	0.121**
		Burn	0.318	0.101**
		No Burn	0.281	0.079*
	Max Humidity		0.394	0.155**
		Burn	0.453	0.205**
		No Burn	0.335	0.112**

* significant to the 0.05 level

** Significant to the 0.005 level

Both Cecidomyiidae and Nematocera abundance showed significant positive linear relationships with maximum and minimum humidity in both the burnt and non burnt edges. Minimum temperature only showed a significant linear relationship with total Nematocera abundance at the burnt edge. All these linear relationships are positive in their direction meaning that the higher the humidity the greater the abundance of both the Cecidomyiidae family and the Nematocera as a whole.

Both groups of data were taken to the next level of analysis. The starting point for all the constants was estimated as in previous sections of this chapter and data were split as it was for the linear regression analysis. The results of the power model are displayed in the table 6.12, below. As before the midpoint of the effect is calculated from the constant B_2 as per the methodologies set out in the preliminary results chapter.

Table 6.12. Power model analysis of transformed Cecidomyiidae and Nematocera abundance (per trap day) against environmental parameters.

Dependent	Environmental Parameter	Treatment	*B_2	r	r^2	†$D_{1/2}$
Total Nematocera	Min Temperature		-	-	-	-
		Burn	-	-	-	-
		No Burn	-	-	-	
	Max Temperature		0.11	0.187	0.035	6.30
		Burn	-	-	-	-
		No Burn	0.037	0.182	0.033	18.73
	Min Humidity		0.039	0.446	0.199	17.77
		Burn	0.041	0.346	0.12	16.81
		No Burn	0.031	0.327	0.107	22.36
	Max Humidity		-	-	-	-
		Burn	0.055	0.469	0.22	12.60
		No Burn	-	-	-	-
Cecidmoyiidae	Min Temperature		-	-	-	-
		Burn	-	-	-	-
		No Burn	-	-	-	
	Max Temperature		0.098	0.226	0.051	7.07
		Burn	-	-	-	-
		No Burn	0.058	0.110	0.012	11.95
	Min Humidity		0.019	0.363	0.132	36.48
		Burn	0.076	0.462	0.214	9.12
		No Burn	0.046	0.341	0.116	15.07

Max Humidity		-	-	-	-
	Burn	0.031	0.587	0.345	22.36
	No Burn	-	-	-	-

- Residual Assumptions not met/iteration limit reached/large standard errors

* positive scaling constant from equation

† Midpoint of the effect; Temperature measured in ºC and Humidity %RH

Minimum temperature failed to fit a line to either the Cecidomyiidae or the Nematocera in either of the treatment edges. Maximum temperature was able to fit a line for both sets of abundances in the non burn data set but in both cases the fit was not acceptable. However minimum humidity fit both abundances at both treatment edges well producing $r^2 > 0.09$. Maximum humidity at the burnt edge was the best fitting of the models for both Cecidomyiidae and Nematocera abundance with r^2 values of 0.345 and 0.22 respectively.

As neither the minimum and maximum temperature nor the minimum and maximum humidity were negative, logarithmic and unimodal models were not assessed. As it was shown previously, without negative independent factors the models find it hard to fit the constants. Therefore the linear and power model results were assessed using the AIC weighting system as before. Only models that met all assumptions were assessed, first grouping all models (burn and no burn) and then grouping by treatment. The results are shown in table 6.13, below.

Table 6.13. AIC weight calculation for linear and power models using environmental parameters as dependent and transformed Cecidomyiidae and Nematocera abundances as independents.

Dependent	Env. Factor	Treatment	Model	RSS	*AIC_c	Δ_i	w_i
Nematocera	Max Temp	No Burn	Power	18.632	-123.04	45.620	8.4E-11
Abundance	Min Humidity	Burn	Power	13.373	-151.56	17.099	1.3E-04
	Min Humidity	No Burn	Power	16.669	-132.61	36.045	1.0E-08
	Max Humidity	Burn	Power	11.149	-167.20	1.456	0.326
	Min Humidity	Burn	Linear	14.971	-144.06	24.605	3.1E-06
	Min Humidity	No Burn	Linear	17.696	-129.67	38.986	2.3E-09
	Min Temp	Burn	Linear	15.297	-138.73	29.928	2.1E-07
	Max Humidity	No Burn	Linear	15.576	-140.65	28.012	5.6E-07
	Max Humidity	Burn	Linear	11.246	-168.66	0	0.674
	Min Humidity	Burn	Power	13.373	-151.56	17.099	1.3E-04
	Max Humidity	Burn	Power	11.149	-167.20	1.456	0.326
	Min Humidity	Burn	Linear	14.971	-144.06	24.605	3.1E-06
	Min Temp	Burn	Linear	15.927	-138.73	29.928	2.1E-07
	Max Humidity	Burn	Linear	11.246	-168.66	0	0.674
	Max Temp	No Burn	Power	18.632	-123.04	17.608	1.5E-04
	Min Humidity	No Burn	Power	16.669	-132.61	8.034	0.018
	Min Humidity	No Burn	Linear	17.696	-129.67	10.974	0.004
	Max Humidity	No Burn	Linear	15.576	-140.65	0	0.978
	Min Temp		Linear	24.552	-199.88	38.701	3.9E-09
	Max Temp		Linear	24.269	-201.33	37.240	8.2E-09
	Min Humidity		Linear	21.233	-218.18	20.401	3.7E-05
	Max Humidity		Linear	18.059	-238.58	0.000	0.999
	Max Temp		Power	24.094	-200.11	38.462	4.4E-09
	Min Humidity		power	20.004	-223.55	15.022	0.001

Cecidomyiidae	Max Temp	No Burn	Power	11.762	-162.60	34.153	2.1E-08
Abundance	Min Humidity	Burn	Power	8.980	-185.81	10.944	0.002
	Min Humidity	No Burn	Power	10.861	-169.46	27.299	6.7E-07
	Max Humidity	Burn	Power	7.959	-196.19	0.564	0.428
	Min Humidity	Burn	Linear	9.170	-186.21	10.543	0.003
	Min Humidity	No Burn	Linear	11.203	-168.99	27.764	5.3E-07
	Max Humidity	Burn	Linear	8.112	-196.75	0	0.567
	Max Humidity	No Burn	Linear	10.804	-172.11	24.645	2.5E-06
	Min Humidity	Burn	Power	8.980	-185.81	10.944	0.002
	Max Humidity	Burn	Power	7.959	-196.19	0.564	0.428
	Min Humidity	Burn	Linear	9.170	-186.21	10.543	0.003
	Max Humidity	Burn	Linear	8.110	-196.75	0	0.567
	Max Temp	No Burn	Power	11.762	-162.60	9.507	0.006
	Min Humidity	No Burn	Power	10.861	-169.46	2.654	0.179
	Min Humidity	No Burn	Linear	11.203	-168.99	3.119	0.142
	Max Humidity	No Burn	Linear	10.804	-172.11	0	0.674
	Min Temp		Linear	16.883	-250.08	21.399	2.0E-05
	Max Temp		Linear	16.123	-255.93	15.550	3.4E-04
	Min Humidity		Linear	14.839	-266.47	5.010	0.071
	Max Humidity		Linear	14.265	-271.48	0.000	0.874
	Max Temp		Power	16.022	-254.59	16.884	1.8E-04
	Min Humidity		power	14.656	-265.91	5.567	0.054

* Corrected AIC used as n/K < 40

Maximum humidity as either a linear model or power model seemed to be the best fitting model out of all the environmental parameters used, at both the burnt and non burnt edges.

Where minimum or maximum temperature had produced a reliable model they were out performed by the humidity parameters.

6.4 Discussion

This chapter aimed to further analyse the use of linear and non linear regression models to investigate edge effects within the study site. The analysis looked at this from three different angles, two related directly to the questions that this thesis is discussing (see section 1.6), that of the effects of height and edge treatment on the populations of Diptera within the study area, and thirdly by using non spatial environmental gradients to explore how seasonality and environment are related to variations in dipteran abundance.

Previous chapters have underlined the importance of height within the canopy in its contribution to seasonal increases and decreases in abundance of Diptera within the study site as a whole. However the contribution of edge treatment (burnt/non burnt) was not so pronounced; therefore using this set of analyses was a good opportunity to look at the underlying effects that burning of the adjacent savannah would have on the relationship between dipteran abundance and its distribution throughout the habitat, and its relationship with the changes in microclimate.

Didham (1997) concluded that with the presence of edge habitat would increase the abundance of some invertebrates as the boundary would allow for an influx of generalist species with a reduction in the forest specialists. Therefore you would expect to see some form of negative relationship between dipteran abundance and forest edge, as abundance would surely decrease as one moves from the edge into the interior.

Of the significant correlations between the studied taxa and distance from the edge all the analysed Calyptrate families and total Calyptrate abundances were negative and this was particularly pronounced in the dry season. The Calyptrate taxanomic group is broadly speaking reliant on decomposing organic matter or live animal hosts to lay their eggs (Goulson et al., 2005). Their adults feed on decaying organic matter, suck blood or in some cases they are pollen and nectar feeders. Although there is evidence of higher tree mortality at the forest edge (Laurance et al., 2002), the literature suggests that despite the decreasing trend in leaf litter decomposition rates from interior to forest edge, there is no overall significant difference between edge habitat and continuous forest (Didham, 1998, Rubinstein and Vasconcelos, 2005). This is despite the increases temperature and reduced humidity that one would find at the edge of the forest.

Perhaps a better explanation for the edge preference of the Calyptrate sub order can be explained from the environmental parameters. Total Calyptrate abundance was significantly negatively associated with both minimum temperature and minimum humidity at the non burnt edge of the forest (see table 6.11). Both of these parameters would be higher towards the internal forest habitat. This shows that the Calyptrate have a definite affinity towards the edge of the habitat that is more likely due to environmental conditions than resource availability. This affinity with temperature and to a lesser extent humidity was an observation made by Goulson et al. (2005), who could predict Calyptrate abundances using temperature changes. Goulson et al. collected Calyptrate samples from six sites measuring weekly temperature averages over a period of three years, and were then able to predict the fourth year population accurately. Other studies such as Barbosa et al. (2010) have shown that even with the exact same decomposing resources available (in this case a decomposing pig carcass), Calyptrate abundance can drop given decreases (>7° C) in abient temperature. There is no information in the literature as to why this is the

case; however one would assume that either larval development or adult metabolic rates are dependent on a particular set of temperature limitations.

In terms of the edge treatment and distance analysis the Calyptrates showed a stronger preference for the non burnt forest edge which confirms the results from chapter 5. Although both edge treatments have a significant association with distance there is a stronger association with non burnt forest edge than burnt edge. The environmental gradients also confirm this with all studied Calyptrate family and total abundances being significantly associated with maximum and minimum temperature, and minimum humidity in the non burnt edge and not with the burnt edge environmental parameters. From the small amount of evidence available it is more likely that Calyptrate spatial patterns are driven by environment factors rather than recourses. As given the exact same resource Calyptrate abundance is higher with increasing temperature (Barbosa et al., 2010). The results from Chapter 5 show that there is a significantly higher minimum temperature at the non burnt edge which would account for these differences and confirm previous studies (Barbosa et al., 2010, Goulson et al., 2005).

In contrast to the Calyptrates the Nematocera family abundances were, with one exception, positively associated with distance from the edge of the forest, meaning that they preferred the forest core to the forest edge (the exception being dry season Cecidomyiidae abundance which showed a slight negative association with distance from the edge). There is very little available literature on edge effects and total Nematocera abundances. Jokimäki et al. (1998) and Bak (2006) have given some limited results specifically on Nematocera but they contradict what is shown here, perhaps due to the small size of the forest fragments studied or the boreal nature of their respective study areas. The results from this study point to a two fold strategy within the Nematocera suborder; one for overall seasonal variations in abundance, and one for the spatial patterns of abundance

within the canopy and from the edge of the forest to the interior. Nematocera abundance is limited by available larval development habitat (fresh water or new growth vegetation for example), however these limitations would not dictate the height within the canopy or the distance from the edge of the forest that the adults are drawn to, as they are mobile and can therefore easily relocate to a more habitable location. Therefore it is more likely that either feeding resources or a particular set of environmental conditions are the attractant to specific areas of the forest either laterally or vertically which would dictate their spatial patterns.

This chapter has investigated total Nematocera and Cecidomyiidae abundance. Previous chapters have shown the importance that height within the canopy plays in seasonal abundance variations within this suborder. Here the use of a combination of linear and non linear models has proved to help understand the relationship between the edge of the forest and the abundance of this suborder. Spearman's correlations showed that there were significant associations between the respective groups and families and distance from the edge, yet the linear regression analysis showed no significant linear relationship. However when the data were reanalysed using the power model suggested by Ewers and Didham (2006), the relationship becomes much clearer.

Grouped dry season and ground and mid canopy dry season Nematocera abundance showed power relationships. The half distances given by the grouped dry season and dry season ground canopy data sets were very similar at 53.32 and 53.31 m respectively. However the dry season mid canopy abundance had a much shorter half distance at only 38.5 m meaning that the greatest increase in abundance was situated closer to the forest edge in the mid canopy than the ground. These results show that the canopy community demonstrates different forms of this edge relationship during the same season, and as there are no significant differences in either minimum humidity or maximum temperature

between the three height classes (grouped data) in the dry season (see Chapter 4), other factors must be contributing to their spatial patterns (feeding resources or small lateral variations in environment for example). Differences in the midpoint of the effect could be caused be several factors; for example the ordinal results (see Chapter 3) showed that both temperature and humidity had differing midpoints depending on the height category. The micro-climate conditions within each height category change at varying rates within the canopy as you move from the edge to the core of the forest. However the grouped mean distance to nearest vegetation results (Chapter 5) show that there is no variation in ground or mid canopy vegetation density between the edge of the forest and the internal control plots, only the high canopy internal control plots have a less dense canopy than its edge counterparts (both burn and non burnt treatments). With treatments combined only the high canopy shows a positive correlation (Chapter 3) with distance from edge, meaning that as the distance from the edge increase only the high canopy becomes less dense and the ground and mid canopy do not change significantly. This is possibly due to the trees sampled in the internal control plots being taller or emergent trees and therefore the changes in temperature and humidity would most likely be a result of more sunlight and wind penetration rather than vegetation structure.

The maximum humidity half distance is 27.73 m in the ground canopy, but then it moves to 40.77 and 57.76 m in the mid and high canopy respectively meaning that the greatest degree of change in maximum humidity is situated further from the forest edge in the mid and high canopy. As mid and high canopy samples are subjected to a greater edge effect then this lag in half distance is to be expected due to their closer proximity to the lateral edge (canopy crown), and as there is only variation in the high canopy distance to vegetation (becoming more open further away from the edge) vegetation structure can not play a significant role in determining the spatial patterns of the Nematocera in the mid canopy. Therefore we must look for other possibilities as to why there are these variations

in spatial abundance patterns. Beyond the obvious preference of damper and cooler conditions that the Nematocera suborder has show in this chapter, there is also the possibility that feeding resources are simply more attractive higher in the canopy and further from the forest edge. The availability of pollen/nectar and other sources of sucrose (Chironomidea and Cecidomyiidae) or blood meals (Ceratopoginidae) maybe more prevalent in the upper canopy or forest core drawing those families higher, or there may be a degree of specialism in food resources which are only available from forest core or upper canopy dwelling plants and animals.

Chapter 5 showed that burning of the adjacent savannah grassland was affecting some of the families studied here. The Muscidae showed the highest affinity in both wet and dry season with treatment from the edge. However the association was always higher with the non burnt edge than at the burnt edge. It is unfortunate that the data would not stand further investigation as the patterns for relationship would have been interesting, as the ordinal level results from Chapter 3 showed that the Muscidae had a significantly higher abundance in the burnt savannah than the non burnt savannah. This suggests that the burnt savannah is more attractive to the Muscidae that the burnt forest edge. These results from inside the forest edge do follow that of Chapter 5 were the Muscidae also showed an affinity for the non burnt edge inside the forest. As was shown in the previous section the association of the Muscidae to the edge of the habitat is a negative one, with higher abundances towards the edge than the core. This means that any anthropogenic changes to the management regime of the adjacent savannah would have an effect on the Muscidae, and possibly other Calyptrates.

The Cecidomyiidae did not show any linear relationship with the edge in either season or under either treatment which follows closely to the Spearman's correlation results where only a weak association with the dry season non burnt edge was shown. Total Nematocera

abundance showed weak associations with the burnt edge in both the dry and wet season and this was confirmed with a linear regression, although there was also a significant relationship at the non burnt edge when the seasonal data were grouped. The power relationship also followed the same pattern with the Nematocera abundance having higher r^2 values for the burnt edge than the non burnt edge.

The relationship between the Nematocera abundance and maximum humidity was strong and positive confirming previous results showing that these organisms are much more abundant during the wet season, due to some of the more abundant family's reliance on fresh water for egg laying and larval development. However this does not explain why they would be more affiliated with a burnt edge as opposed to a non burnt edge.

Using the Cecidomyiidae as an example, we know from previous research that they are gall forming invertebrates that prefer new growth vegetation to form their galls (Boukili et al., 2007), and that the start of the wet season signifies the greatest abundance of leaf galls (de Araujo and dos Santos, 2009). Burning of the savannah provides an ideal habitat for this, as there will be a significant rise in new growth vegetation for the Cecidomyiidae to utilise after the savannah is burnt. It is unlikely that the Cecidomyiidae are utilising the savannah grassland specifically (see Chapter 3); however fire tolerance of tree species at the forest edge would be more pronounced than in the interior, because if not the boundary of the forest would be continually moving towards the core. One strategy used by fire and disturbance tolerant tree species is re-sprouting after fire disturbance (Bond and Midgley, 2001), this would increase new vegetative growth and therefore available gall forming habitat for the Cecidomyiidae. Once emergence has taken place, adult Cecidomyiidae could then move further into the forest core and higher into the canopy where environmental conditions and feeding resources are more appropriate, and subsequent generations can be produced.

So far the importance of environmental factors in the magnitude, movement and distribution of Diptera abundance has been made clear through both analysis of these data and through review of other studies. We know that Diptera replace bees (Hymenoptera) as pollinators as the climate becomes wetter (see Devoto et al. (2005) for example), and it has been shown that in the studied habitat dipteran abundance is significantly higher in the wet season than in the dry season. Previous chapters have also pointed to a relationship between the edge of the forest and changes in temperature and humidity confirming previous research into this area (Laurance et al., 2002, Bierregaard et al., 1992). Therefore using environmental parameters as a gradient of edge effects and vertical stratification could be more productive than spatial factors alone.

Previous analysis (see Chapter 3) showed that minimum and maximum humidity and minimum temperature all increased with distance from the edge of the forest, and that maximum temperature decreases closer to the forest core. This information combined with the correlations performed in this chapter can show whether a family or taxanomic group is edge affiliated or core affiliated by using the environmental rather than spatial parameters. For a family or suborder to be edge affiliated there would need to be a positive association with maximum temperature (as temperature increases towards the edge) and a negative association with the other three environmental gradients (as they decrease towards the edge), and core affiliation would have the opposite associations. Using this premises all the Nematocera families are core affiliated, with all the above conditions met, were as the Sarcophagidae, for example, fit the opposite situation and therefore can be considered an edge affiliated family.

Using this set of criteria removes the rather ambiguous categories of wet and dry season (due to shifting weather patterns and possible climate change), and means that you can

collect data cross seasonally rather than in a specific time period and still be able to look for variations in measurements based on knowledge of the changes in seasonal environmental conditions and in spatial micoclimate conditions. Knowing that, for example, maximum temperature is significantly higher in the dry season than the wet, and that forest core maximum temperature is lower than forest edge, means that at the lower maximum temperature in this analysis represents wet season and forest core, where as the higher maximum temperatures represents dry season and forest edge. This can also be combined with vertical stratification, where maximum temperatures are higher in the high canopy and lower in the ground canopy. For example Sarcophagidae abundance (see Chapter 4) has an affinity with the higher canopy and not with the ground canopy. So by using this one environmental factor we could predict that one or more of the following statements are correct; a.) Sarcophagidae abundance is higher in the dry season than the wet, b.) Sarcophagidae abundance is higher at the edge of the forest than the interior, and/or c.). Sarcophagidae abundance is higher in the upper canopy than at ground level. Therefore by just investigating the affiliation that these families have with microclimate their spatial patterns can be to some degree inferred.

The regression models used on the Cecidomyiidae and Nematocera abundances showed similar results to the spatial gradients tested previously. The linear model was again the best performing model within the analysis, especially for maximum humidity. The power model was only able to compete with the linear on a few occasions again when using maximum humidity as a gradient but only when edge treatment was taken into account. When all edge treatments were grouped the linear model was the only acceptable model of those tested (see table 6.13).

The simplest explanation for the power model not fitting as well here as it did in previous sections was the relative shortness of the independent scale. For example the maximum

temperature only varies between ~30 ºC and ~45 ºC, only leaving a 15 ºC variation. The humidity scales are longer with maximum humidity varying from ~ 30 RH% to 100 RH% which perhaps accounts for its higher level of performance in the AIC context of the other models.

What this chapter has shown is that there are detectable edge effects within the study site, and that those effects change according to the specific family or suborder that is being analysed, and according to what particular spatial aspect is being investigated. This chapter has also underlined the importance of understanding the environmental gradients that are present within the study site and that once the underlying relationships and associations are understood can help to predict abundance levels of the Diptera present within the habitat.

Chapter 7: Discussion; Spatial and temporal patterns driving the abundance of Diptera in a Nigerian tropical forest

7.1 Introduction

Arthropods are major suppliers of ecosystem function, providing key ecosystem services to maintain functionality within the confines of a habitat. Variations in community structure, diversity, abundance and richness of arthropods can have far reaching effects, even outside of that habitat (Kremen et al., 2002). This is particularly pronounced in tropical forests, where arthropods have evolved a greater degree of specialisation than in higher latitudes (Dyer et al., 2007). Specialisation leads to increased exploitation of specific niches within the habitat, which can often be determined by only small changes in environmental conditions, or the presence of resources specific to a particular species at a particular stage of their life cycle. Variations in these levels of arthropod abundance and community structure within such a specialised environment can change the way in which a habitat functions and grows, whether through the natural course of a successional habitat, maintaining the cyclic balance of a climax habitat, or recovery from a detrimental event (Dickie et al., 2011, Dijkstra et al., 2011).

The literature has pointed to a close link between spatial and environmental gradients, with one ultimately influencing the other (Laurance et al., 2002, Bierregaard et al., 1992), and the interactions with organisms within a specific habitat (Kitching, 1972, Bishop et al., 1996). This thesis has brought together spatial, temporal and environmental factors and investigated how their effects, both separately and when in conjunction with each other,

impact the target taxa in terms of abundance and richness (see Chapter 4). In the context of global declines in biodiversity, climate change, anthropogenic manipulation and destruction of natural habitats, the importance of the effects of spatial and temporal factors of the abundance of key orders of invertebrates is highly relevant.

This thesis has used a bottom up approach to its analysis, much in line with concepts of community ecology, where factors that increase or decrease the abundance and richness of species are investigated (Loreau, 2010). By using the methodology set out in this thesis, even with the limitations of habitat replication mentioned in Chapter 2, it has been possible to investigate abundance and richness at both the micro and meso scale. This thesis aimed to investigate three spatial conditions and the effect of temporal variations on those conditions. Spatial conditions were split into three categories; height within the canopy (vertical stratification), distance from the edge of the forest (edge effects), and forest edge treatment (savannah burning). These spatial conditions were then analysed in conjunction with environmental factors and seasonal partitions to investigate the effect that these combined factors had on the abundance, and in some cases richness, of Collembola and Diptera populations within this Nigerian tropical forest.

Because of the way each of the three spatial conditions interacts with environment this chapter will intertwine temporal and environmental factors around the three structural components. As the previous results chapters have treated each of the spatial condition separately, this chapter will discuss the overall effect of the three spatial conditions and environmental factors from the point of view of the suborders, groups and families that have been analysed. Thus combining all the information gathered throughout this thesis to draw reasoned conclusions. As the analysis of collembolan data was only conducted and discussed at the ordinal level (Chapter 3), it will not feature here. Therefore this chapter

will concentrate only on the dipteran community and the effects of spatial and temporal variations on its abundance and richness.

7.2 Spatial and temporal effects on the abundance of Acalyptrates and other Brachyceras in a Nigerian tropical forest

Seasonal analysis of the Brachycera and Acalyptrate showed no significant difference in their respective abundances, although there was a negative trend in association with the wet season (see fig 4.4). However once the analysis took into account height within the canopy, seasonal changes in the spatial positioning becomes apparent and significant. Both groups followed the same pattern of no significant changes in the abundances found in the mid and high canopy between the two seasons, but the ground canopy abundance significantly reduced in the wet season (see fig 4.5).

If the results of the environmental correlations with the Brachycera and Acalyprates are then taken into account, there is a significant association with maximum humidity (see table 6.10). So in the dry season both have a preference for the ground canopy due to the increased humidity, however during the wet season when humidity is much higher throughout the entire vertical column their preference is for the higher temperatures and lower humidity found in the upper canopy. However as their abundance does drop (although not significantly) during the wet season it is not entirely clear as to why this would happen.

Phoridae (Brachycera) are known to lay their eggs in dung, carrion and are sometimes parasitoids (Stubbs and Chandler, 1978, Mankowski and Morrell, 2003). These life histories would explain their dry season preference as the availability of substantial

amounts of animal dung and carrion deposited above the forest floor would be limited due to the effects of gravity; however these resources would be readily available on the forest floor. Other dung and carrion associated arthropods (dung beetles for example) have a significant relationship with the number of non flying mammals present within the habitat (Estrada et al., 1998), where again one would assume a majority of dung and carrion associated with non flying mammals would be deposited on the forest floor rather than in the canopy. There are also reports that increases in temperature (exposure to +39º C for a period of 48 hrs) can inhibit the ability of some species of Phoridae to emerge from host invertebrates (Mankowski and Morrell, 2003), meaning that during the dry season the lower temperature of the forest floor would be more accommodating; however once the wet season starts the temperature drops significantly in the higher canopy making this stratum more acceptable for parasitoid species.

The Phoridae also have an affinity with the forest core as their association with distance is always a positive one, showing that they prefer the forest core to the edge. Once treatment is taken into account the Phoridae only show a significant positive association at the burnt edge. A positive association denotes a family/suborder/group that prefers the core of the forest to the edge, so as distance from the edge increases so does the abundance. During the dry season both minimum humidity and minimum temperature are lower at the burnt edge, so the Phoridae are moving further into the forest core where the minimum temperature (night time) and minimum humidity (daytime) are higher, which would better suit their optimal environment (Mankowski and Morrell, 2003).

Of all the Brachycera sampled the Phoridae represented the family with the highest abundance; however, the Brachycera follow the same pattern, moving away from the burnt edge in to the forest core, but not being affected by the non burnt edge. Whether it is the act of burning itself or the environmental variations that that it has caused that has

influenced the spatial patterns of this group is not clear. What is clear is that there is an effect that can be measured and patterns that have developed due to this event, which have created an edge effect within this sub order forcing the community further into the forest away from the burnt savannah edge. Ecologically this implies that the nutrient cycling which is associated with the life history of this group could be impeded by this act, although it is likely that the open niche which is left behind could be filled by other organisms or indeed other Diptera families, Muscidae for example, which have an affinity with the environmental conditions found at this edge and are associated with dung and carrion.

In contrast to the Brachycera the Acalyptrate change their core or edge affiliation between the seasons, with a negative association to distance from the edge during the dry season (edge affiliation) and a positive association during the wet season (core affiliation) (table 6.1). As with the Brachycera only the ground canopy abundance decreases significantly between the seasons, with mid and high canopy abundances varying very little. This is reflected in the correlations with distance from the edge with the ground canopy having a negative significant association during the dry season, and then the mid canopy wet season abundance has a positive association with the distance from the edge. So the abundance shifts from the edge in the dry season to the core in the wet (table 6.1). The relative stability of the mid and high canopy Brachtcera and Acalyptrate communities across the seasonal divide shows that the higher canopy is a very important habitat for these groups helping to maintain their abundance in both the dry and wet season.

Taking treatment into account, we see that in general the Brachycera abundance is positively correlated with distance from both burnt and non burnt edge, showing a forest core association when treatment is accounted for. However, taking seasonality and treatment into consideration there is only core association at the burnt edge in the dry

season, which would indicate that an edge effect is introduced immediately after the savannah has been burnt, yet by the start of the wet season there is an edge effect at both burnt and non burnt edges.

One of the most studied members of the Acalyptrates are Drosophilidae. This family is mainly reliant on fruits and fungi as their larval hosts (van Klinken and Walter, 2001). However understanding the phenology of fruiting events in the tropical forest is problematic, with many factors understood to affect the timing of such events (Chapman et al., 2005, Snow, 1965). Therefore linking abundance of this particular family to particular fruiting events throughout the habitat or over the seasonal change would be impractical in this thesis. There have, however, been indications that some species of Neotropical Drosophilidae may migrate from savannah to forests when climatic conditions are no longer favourable (Tidon, 2006). The family have also been suggested as a bioindicator for habitat quality, due to the changes in community assemblage from disturbed to pristine habitat (da Mata et al., 2008). Unfortunately as taxonomic identification of this order has not been available in this thesis it would be difficult to determine how the community changes between the two contrasting edges and indeed between the edge of the habitat and the forest core. However, as there is evidence that some species show migratory behaviour (Tidon, 2006), it can be suggested that the shifts in abundance through the lateral and vertical gradients could be a result of similar behaviour, either due to environmental conditions or due to shifting patterns in fruiting phenology.

7.3 Spatial and temporal effects on the abundance of Calyptrates in a Nigerian tropical forest

7.3.1 Total Calyptrate

The change in seasons had the most significant effect of the Calyptrate as a whole as well as the families investigated within it. With abundance and richness being significantly higher within the dry season, the affinity to a particular set of environmental conditions throughout this thesis has been quite consistent. The Calyptrate showed no preference for a particular height within the tree canopy in either season; however the change in abundance and richness at ground and high canopy between seasons was consistent with abundance always significantly decreasing in the wet season.

Although the total Calyptrate abundance showed no significant difference in the mid canopy between seasons, there was a significant decrease in both the ground and high canopy abundances in the wet season. Barbosa et al. (2010) showed that necrophagous species had a higher abundance during the summer months in Brazil, and one would assume that most necrophagous food and reproductive items (dead and dying organic matter for example) would be found in the ground canopy, having fallen from the higher canopy or dropped directly to the forest floor, yet their abundance in the high canopy is not significantly different from the ground canopy. Food and reproductive resources therefore do not account for the significant decrease in abundance in the high canopy. The correlations to environmental parameters showed an edge preference at the non burnt edge, with associations being negative for minimum temperature, minimum humidity and maximum humidity, and positive for maximum temperature. These environmental associations show that the higher canopy strata would be preferred due to more agreeable

environmental conditions during the dry season and that the ground canopy due to the increase feeding and larval resources.

When seasonal data were grouped the Calyptrate showed an edge preference at both treatment edges; however when season was taken into account there was no edge or core preference at the burnt edge during the wet season. The environmental conditions become much more homogenous in the burnt edge (see fig 5.7), and there are no significant differences between the two treatment edges in any of the environmental parameters analysed during the wet season, although the internal forest area showed significantly higher maximum temperature and significant lower minimum humidity. There is also no significant difference between overall abundance between the two treatment edges or between the treatment edges and internal control plots during the wet season. Therefore these homogenous environmental conditions across the forest from edge to core during the wet season mean that there is no need to prefer the edge as the conditions are continuous throughout the habitat. Whereas in the non burnt edge the optimal conditions are pushed towards the edge of the forest meaning that the Calyptrates show a preference for it.

These results suggest that the less dense understory burnt edge habitat does not result in an edge effect in the Calyptrate. Whereas when the habitat is denser, like it is at the burnt edge, the edge effect is more pronounced. As has been discussed in other sections of the thesis, the differences in ground canopy vegetation density is not necessarily due to the burning of the adjacent savannah, although it cannot be discounted. Bucini and Lambin (2002) did show that late season burning did reduce vegetation cover in the adjacent forests, and therefore it is entirely possible that continued late season burning has reduced the vegetation density at the burnt edge over time.

If the burnt edge continues to be subjected to late season burning then the forest edge would presumably become even less dense over time, increasing the opportunity for a more scrub/savannah habitat to develop. This would ultimately change not only the physical structure and community of the vegetation but also the organisms that inhabit it. With more exposure to sunlight and wind the humidity at this edge would drop and the temperature would increase. These are favourable conditions for this group of Diptera and therefore may increase there abundance. However the negative impact of this increase would entail a higher parasitoid and parasitic infection rate from this group of Diptera, which would then negatively impact their hoist species.

7.3.2 Sarcophagidae

The Sarcophagidae family contributed to 22.5% of total Calyptrate abundance, but unlike other families in this group only comprised of a single genus, *Senotainia*. This genus are known parasites/parasitoids of Hymenoptera (both Sphecidae and Apidae) and Lepidoptera (Noctuidae for example) (McCorquodale, 1986, Thippaiah and Kumar, 1999, Pinzauti and Santini, 1995), and therefore very dependent on the presents of its host species for larval development. This dependence on the presence of host species explains the significant decline in abundance during the wet season. The honeybees, for example, will predominately visit the forest during the dry season and then the savannah during the wet season (Lobreaucallen and Damblon, 1994), therefore increasing available larval resources in the forest during the dry season which in turn would increase the dry season abundance.

The presents of a larval resource is unlikely to influence the choice of forest strata, treatment, or distance from the edge which the adult Sarcophagidae would inhabit. These factors are more likely due to either adult feeding resources or environmental conditions. Unfortunately there seems to be little or no published research into the feeding or foraging

behaviour of the adults of this genus, rather published data concentrates on the larval parasitism of the numerous invertebrate and vertebrate hosts. There is evidence to suggest that the adult Sarcophagidae are nectar feeders (GarciaFranco and RicoGray, 1997), and would therefore be drawn to areas of the forest that include this resource. Flowering in tropical forests tends to take place in the dry season, which again accounts for the higher abundances seen at this study site (Chapman et al., 1999), however would this account for the preference towards the edge of the forest that this family, and in fact the group, seem to be showing. Studies from the North America have shown that in some flowering species there is a distinct edge effect impact on flowering, with flowering decreasing further away from the edge of a forest (Landenberger and Ostergren, 2002). It must be stated, however, that these results were from a clear cut edge in a temperate forest; but it still gives the possibility that there may be some form of edge effect on the flowering species within the Kwano forest. The same could be true of the higher canopy, where there would be an increase in vegetation and sunlight (much like the lateral edge) increasing the level of flowering in the mid and high canopy, and therefore increasing its attractiveness to the Sarcophagidae. This would increase the feeding resources for the Sacrophagidae at the edge of the forest and therefore account for their preference for it.

The Sarcophagidae showed an edge attraction at both burnt and non burnt edges, however once season was accounted for the results show that there is a significant association with the burnt edge in the dry season but not the non burnt edge, and then this reverses in the wet season, with the association switching to the non burnt edge. All of the environmental parameters also point to this association at the non burnt edge, with minimum temperature, minimum humidity and maximum humidity all having a negative association and maximum temperature having a positive association, both when treatment data is pooled and when it is split between the two treatments.

The differences in the environmental conditions between the two treatment edges could point towards the reasons behind this affiliation. In the dry season the burnt edge had a significantly lower minimum and maximum humidity and minimum temperature than the non burnt edge (fig 5.6). This means that the environment was much dryer at the burnt edge, although there was no significant difference between maximum temperatures between the two treatment edges. Correlations between the Sarcophagidae and the environmental conditions show that there is an association with these conditions and it is probably this that is attracting the Sarcophagidae to the burnt edge.

The question that remains is whether the process of burning at the edge of the forest is the main contributing factor to the dryer environment found there. The results of the distance to nearest vegetation analysis showed that there was a significant difference in density of habitat in the ground canopy. With the burnt edge having a more open habitat which would affect the environment, increasing the abundance of light and breeze in the forest structure reducing the humidity and night time temperature (see previous section).

In conclusion, the analysis has shown a strong correlation to a dry environment, with increased feeding resources determining the association of adult Sarcophagidae to particular spatial preferences, and that the seasonal availability of larval hosts determines the higher abundance seen in the dry season. With the strong possibility of global climate change disrupting the balance between wet and dry season (see section 7.5) both the pattern of flowering plants and availability of larval hosts may change dramatically which would have serious implications on both the abundance and spatial patterns of this Family.

7.3.3 Muscidae

The Muscidae sampled during this project represented 10 genera and 17 species (8 new or unknown), and contributed to 23 % of overall Calyptrate abundance. Of all the families studied, the Muscidae showed the most significant reaction to the burning of the adjacent savannah, and, much like the Sarcophagidae previously, show a strong association with the edge of the forest. However, the Sarcophagidae were also highly correlated to environmental parameters, whereas the Muscidae are not (table 6.1).

From the literature there seems to be no fixed seasonal period of high abundance across Muscidae genera. For example there are accounts of the warm dry seasons in New Zealand being preferred by native *Masca* species (Heath, 2002), wet season for *Stomoxys* in Thailand (Masmeatathip et al., 2006), and the warm wet season in parts of Brazil (Mendes and Linhares, 2002). But as we learnt from the Sarcophagidae family, abundance was always closely linked to the presence of larvae hosts and resources, so is this the same for the Muscidae. A vast majority of the available literature on this particular family of Diptera is concentrated on their presence in commercial livestock dung and physically on the animal. Muscidae are vectors for many pathogens and have therefore been studied intensely for this reason (Antoniazzi et al., 2011, Pitzer et al., 2011, Mwamburi et al., 2011). The family are generally considered to be dung, decaying organic matter and live organic matter feeders, with only the *Stomoxys* being the exception as blood suckers. Therefore their feeding resources and larval development resources should be available year round.

The results from this thesis show a very clear and significant preference for the dry season in both forest and savannah habitats. However there was no correlation between the

Muscidae abundance and any of the environmental parameters analysed. One parameter that was not analysed was rain intensity, and here we do find a significant correlation, r_s = -0.240, $p < 0.001$. The literature does show a relationship with rain and some genera of Muscidae. However the relationship is positive, for example *Stomoxys* show a positive relationship with March rainfall in the US (Mullens and Peterson, 2005). In the Nigerian forest studied in this thesis, the abundance Muscidae is not just significantly lower in the wet season, it was almost nonexistent with <10 individuals sampled over the two wet seasons.

Therefore given the lack of empirical evidence to suggest otherwise, we must assume that seasonality is purely a result of rain and not the presence of feeding or reproductive resources, or other environmental parameters. This is a strange result, as one would assume that if the absence of rain is the overriding factor to dictate the abundance of this family of Calyptrate, then secondary factors such as humidity and temperature would also play a role; however as the results show the adults are not affected by these parameters. The almost complete lack of individuals sampled during the wet season suggest that there is some form of larval relationship that has a dry season association, which could be connected to environmental conditions, yet once emerged as adults these environmental constraints are no longer significant and therefore the adults show no preference for a particular set of environmental conditions.

The abundance of the Muscidae in the dry season forest and savannah has also shown an interesting outcome. The analysis showed that during the dry season the Muscidae had a significantly higher abundance in the burnt savannah compared to the non burnt savannah, and in the non burnt forest edge compared to the burnt forest edge. Taking the habitat as a continuous gradient across the forest boundary, these data show that if the adjacent savannah is burnt then the Muscidae are likely to move out of the forest and into the

savannah, where as if the savannah is left without burning then the Muscidae will stay within the forest boundary. The correlations with the environmental parameters showed that there is no association with a warmer dryer habitat despite this family's preference for the dry season. However there maybe a higher abundance of decaying matter (although burnt) within the burnt savannah in which the Muscidae could feed. In truth there is little evidence from this data set to show why the Muscidae have this preference for the burnt savannah habitat over the non burnt, or why they would prefer the burnt savannah to the adjacent forest edge.

7.4 Spatial and temporal effects on the abundance of Nematocera in a Nigerian tropical forest

7.4.1 Total Nematocera

Throughout this thesis the Nematocera suborder has undergone a majority of the analysis performed. This has been due to the fact that this suborder has the highest abundance of all the analysed groups, with 81.9 % of total abundance over all samples and all years, and although the data were not normally distributed a $\log_{10}(x + 1)$ transformation created normality within the data set. Unlike the Calyptrate in the previous section, the Nematocera significantly increased their abundance in the wet season. This suborder also showed the most significant reaction to spatial positioning in combination with seasonal changes. Although not quite as obvious as the Calyptrates, there was some reaction to burning in the adjacent savannah but due to the differences in edge effect rather than in overall abundance found in the two varying habitats.

Families such as the Cecidomyiidae Ceratopogonidae, Sciaridae and Chironomidae showed a significant increase in abundance in the wet season. The only family analysed to show the opposite effect was the Mycetophilidae, whose abundance significantly decreased during the wet season. This follows previous research that has suggested that the Mycetophilidae (fungus gnats) replace aquatic associated species, such as the Chironomidae, during the warmer months (Progar and Moldenke, 2002). The Sciaridae (also fungus gnats) rely more on larval feeding resources, such as new growth vegetation and fungus, and are therefore more abundant in the wet season (Harris et al., 1996). For the other analysed families there are explanations for the seasonality shown, Chironomidae and Ceratopogonidae are aquatic associated species, and the Ceratopogonidae are also susceptible to extreme lower temperatures (Bishop et al., 1996, Kitching, 1972), hence their affinity with the wet season as minimum temperature in the wet season is significantly higher than the dry season. The affinity with the wet season is also apparent from the correlations with environmental factors, with a significant negative association with maximum temperature, and significant positive relationships with both minimum and maximum humidity.

There were significant differences in all five analysed families in the abundances found at each height category, and significant differences in the abundances between seasons. The total Nematocera abundance was significantly higher in the ground canopy during the dry season than both the mid and high canopy. However during the wet season the ground canopy did not show any significant increase or decrease, but both the mid and high canopy significantly increased in abundance, and therefore had a significantly higher abundance than the ground canopy during this time. The dry season reliance on the ground canopy is again reflected by the association with particular environmental parameters. With the ground canopy having higher humidity and lower temperatures during the dry season, and these are the preferred conditions for a majority of the families analysed. This

also provides further evidence of the forest core association with again lower temperature and higher humidity found in this habitat during the dry season.

This seasonal increase shown in the overall abundance is only found in the higher canopy, this is reflected by the Cecidomyiidae, Ceratopogonidae, Chironomidae and the Sciaridae (Sciaridae also had significant increase in the ground canopy abundance). The lower temperatures and higher humidity found in the upper canopy (mid and high) during the wet season (as opposed to the dry season upper canopy) opens up this habitat for the Nematocera to exploit. Feeding resources for these families may also be more prolific in these strata during this time of year, with increases in nectar and honeydew (Cecidomyiidae and Chironomidae), and in prey species (Ceratopogonidae) (Burtt et al., 1986, Swanson and Adler, 2010, Bawa et al., 2003). Available larval resources are also increased in the wet season for both the Chironomidae and Ceratopogonidae, both being associated with aquatic or near aquatic larval habitats (Kitching, 1972, Uslu and Dik, 2010)

All of these factors point towards a clear association with the wet season on the grounds of environmental preference, feeding resources, and abundance of available larval habitat. However this association is completely played out in the mid and high canopy. When the data were split between rain categories (0, 1-10, 11-30 and 31-80 mm), at no point did the abundance in the ground canopy show any significant increase or decrease. In fact the abundance in the ground only noticeably increased (but not significantly) during days with rainfall above 30 mm, and probably just reflects the difficulty of flying in the upper canopy during heavy rainfall.

The total Nematocera did show edge effects in both the correlation analysis and in the regression analysis. Mid and high canopy abundance showed a forest core affinity, where as the results form the ground canopy show an edge affinity. However once the savannah

samples are removed from the ground canopy data set there appears to be no edge effect in the ground canopy. These association are confirmed with the linear regression, with again both the mid and high canopy having significant linear relationships but not the ground.

In the dry season the community seem to be driven by environmental parameters where lower temperatures and higher humidity dictate where their abundance is found with the forest (ground canopy and forest core), where as in the wet season when the environmental factors become less variable within the forest, feeding resources become the main component of determination for spatial patterns, and an increase in available larval habitat drives the rise in overall abundance.

When taking treatment into account only the burnt forest edges show a consistent edge effect. Linear and power models showed a significant relationship and the correlation confirmed that these are positive in both seasons. As with the Calyptrates we cannot discount a natural difference in forest structure, but the evidence does support a greater abundance in the edge of the forest, with more gall vulnerable vegetation species at the burnt edge (Bond and Midgley, 2001, Boukili et al., 2007, de Araujo and dos Santos, 2009).

The results presented in this thesis for the Nematocera suborder are consistent with previous research into their various families. There is a heavy reliance on both feeding and larval resources that seem to dictate when the abundance is greatest and where that abundance is most likely to be located within the habitat. Larval resources and optimal environmental conditions account for the timing of major emergence events, and feeding resources together with preferred environmental conditions created a spatial segregation which is followed by most of the families analysed. However, as was mentioned in the previous chapter, the consistency in which these patterns follow a set of particular

environmental parameters is also quite clear. There is an obvious relationship between humidity and spatial placement in the dry seaosn, and the timings of the rains may have an effect on emergence activities. For example the field research was able to record an apparent emergence event during the second field season, when ~150 Chironomidae adults were captured in a single 24 hr period from a single trap. Given that the average for this family was ~ 4 per trap day, this could signify a significant emergence event. This coincided with the first heavy rains of the season (within one week), which could therefore be a signal for overwintering pupae to hatch or for adults to increase egg laying activity. This is a single occurrence and has not been verified through repeated sampling, but given the weight of the evidence that the Chironomidae are significantly affiliated with the wet season, it does make for a logical conclusion.

The overriding implication for this family is that their abundance and spatial patterns are driven by both the environment and the availability of resources either for feeding or reproduction. Both are closely linked with the environment and specifically the change from an environmentally driven community in the dry season to a resource driven community triggered by the start of the rains. As the abundance in the ground canopy does not change between seasons, we can assume that the carrying capacity for the ground canopy is reached in terms of feeding resources and that the higher canopy is unavailable due to adverse environmental conditions in the dry season. However once the rains start the ground canopy can not support the increase in abundance and therefore the community look to the higher canopy to feed once the environmental conditions are more conducive. In effect the environmental conditions are removed from the equation once a certain threshold in temperature and humidity is reached, and the abundance is then dependent on the only amount resources necessary to sustain the population.

It is clear that there is further research needed to clarify these relationships and affiliations as this research has been limited by the lack of taxonomic identification beyond the family level. It is hoped that the samples collected in this research will be further analysed by taxonomists so that a finer level of species richness can be obtained. This will help to define both the seasonal and spatial differences that have been shown in this thesis.

7.4.2 Cecidomyiidae

The Cecidomyiidae were the most abundant family sampled within the study site. They represented over 40 % of the total Diptera abundance and therefore many of the relationships and trends that have been shown in the larger scale analysis have been due to the way in which the Cecidomyiidae have reacted to the changes in environmental conditions, the structure of the forest, or to the presence of feeding, larval and reproduction resources.

The Cecidomyiidae are an important economic pest in agricultural systems, damaging crops by forming galls on their leaves for the development of their larvae (Boukili et al., 2007). There is therefore quite a substantial amount of research into their ecology and reproductive cycle. These sources of information can easily be applied to more natural environments in which they are found. This thesis has consistently used the Cecidomyiidae to analyse the effects of spatial positioning and seasonality as the data could withstand deeper and more substantial analysis.

The general themes recurring in this family are the need for optimum vegetation conditions for gall formation, and the need for a set of environmental conditions in which the adults can feed and breed. These optimal conditions entail a cool daytime relative temperature and high humidity, and a preference for new growth vegetation for gall formation and

therefore larval development (Boukili et al., 2007, Gillespie et al., 2000). These preferences therefore help predict where and when the Cecidomyiidae will be more abundant, for example, the low canopy during the dry season, or the mid and high canopy during the wet season.

As with the total Nemotocera abundance the Cecidomyiidae increased their abundance significantly during the wet season. And much like the rest of the suborder the increases were all seen in the mid and high canopy. During the dry season the ground canopy held a significantly higher abundance, but once the rains started the abundance in the mid and high increased matching that of the ground canopy. Interestingly there was again no significant variation in the abundance in the ground canopy once the rains had started. The dry season results from this analysis follow in the same pattern as the environmental conditions. The correlation analysis showed that the family prefer cooler and more humid conditions; therefore the ground canopy is preferred during the dry season. This was further confirmed by the internal control plots having a significantly higher abundance than both of the edge treatments, with no overall difference between the burnt and the non burnt edges.

Once the rains have started the temperature and humidity in the upper canopy become more suitable for the Cecidomyiidae, their abundance increases. Although, as was discussed in the previous chapter, there are other influences that could drive the Cecidomyiidae higher up in the canopy. The negative correlations with maximum temperature and positive correlations with minimum and maximum humidity also point towards a core affiliated family. As with the total Nematocera the ground canopy shows a negative association with the edge of the forest and a positive in the upper canopy, but again as with the total Nematocera once the savannah samples are removed from the analysis there is no significant association at the ground canopy in either season.

There seemed to be very little reaction to burning in the adjacent savannah, with no significant difference between the two edges and no real relationship of any kind exposed by the regression analysis (section 3.6.2 and Fig 5.10). There were some weak relationships when just height is taken into account with mid and high canopy samples showing power or logarithmic patterns, however the ground canopy abundance showed no edge effects at all. Edge core contrast effects are much stronger in the lower canopy, shown by the differences in the mid point of maximum temperature and minimum humidity between the ground canopy (close to the edge) and mid and high canopy (towards the core), implying that the ground canopy environmental edge effect has less penetration than the mid and high canopy. Therefore the Cecidomyiidae are quite content to inhabit this particular stratum of forest closer to the edge than in the mid and high canopy even though there is a substantial linear relationship between distance from the edge and humidity and maximum temperature during the dry season.

Much emphasis has been put into the gall forming ability of this family of Diptera and its links to abundance and spatial positioning in this thesis. It is known that there is a pheonological window which the Cecidomyiidae use to deposit their eggs (Imai and Ohsaki, 2009, Boukili et al., 2007); however this does not explain their prevalence during the dry season as the vast majority of new vegetation growth is in the wet season (Chapman et al., 2005). The Cecidomyiidae have the highest abundance of all the families studied in the dry season, and although there is evidence from the literature to suggest that some floral species exhibit dry season vegetation growth (Aide, 1992), the extent of this is likely to be low and specialised. The Cecidomyiidae larvae however can also be faunal parasites and parasitoids, preying on aphids and spider mites as hosts (Muratori et al., 2010). So a differing larval development strategy may be utilised during the dry season, with the community utilising an arthropod parasitic larval development strategy in the dry

season rather than the floral parasitic strategy of the wet season. However this would need to be confirmed through further taxonomic identification.

Once the rains start and the pheonological and environmental conditions and potential arthropod host species abundances increase, the Cecidomyiidae can increase their abundance dramatically with a much wider range of host plants and arthropods displaying the right phonological condition or higher abundance. However the presence of increased larval habitat should not dictate where the adults are found within the forest system, as an adult's flying range is not constricted by this. It is more likely that the adults feeding behaviour would dictate where is would be found in the canopy. As adults the Cecidomyiidae can be pollen feeders (Yuan et al., 2007) one would look for where the abundance of pollen is going to be greatest. Tropical forest plants will often rely on only a few specific pollinators so that competition between plants is minimised and pollination is therefore maximised, these plant traits are specialised in terms of mechanical, temporal and ethological niches (summarised by Zjhra (2008)). Therefore with an increase in potential pollinators caused by the onset of the rains plants would produce these feeding resources in order to maximise their pollination rates.

This spatial pattern and abundance in the Cecidomyiidae follows closely to that of the total Nematocera, where an express shift in strategy from environmental constraints in the dry season to resources limitations in the wet season was evident. Similarly here we see that total abundance in the dry season is limited to available larval development medium, and that environmental conditions control their spatial patterns. In the wet season there is a significant rise in abundance due to the rise in available larval habitat, and because the higher canopy environmental conditions become more conducive the community can feed higher in the canopy. Yet again there is no variation in the ground canopy abundance between the two seasons, suggesting a carrying capacity is in effect.

To conclude it is a combination of environmental, phenological and behavioural traits that cause the Cecidomyiidae to vary their abundance and sift the concentration of abundance within a particular season or between two seasons. The distinct changes in environmental conditions within this forest system (one dry season and one wet season per year) give the perfect opportunity to study how the seasonality of the habitat drives both the abundance and spatial ecology of this family. The physical presence of gall formations on vegetation also present a potentially quantifiable method to validate the collected information presented in this thesis. Further investigation of this family, specifically in gall formation/host parasitism, feeding behaviour and plant interactions would create a clearer picture of the ecology of seasonal tropical forests.

7.5 Implications of results in a changing world

In West Africa the monsoon climate dominates the rain patterns and therefore the temperature, humidity and rainfall that are experienced in the region. The Kwano forest follows the seasonal pattern of one dry season (from roughly mid October to mid March) and one wet season (mid March to mid October) annually (see section 2.3.1 for a formal description of climate at the site). The rain brought by the West African monsoon is facilitated by increasing solar radiation which in turn raises sea surface temperatures in the Gulf of Guinea during the spring months (the hottest part of the year); this increases the amount of surface water evaporation forming large clouds which then are forced across the West African region by the ensuing westerly winds. Once these clouds reach landfall they start to deposit water on the land and vegetation, continued terrestrial evaporation and the continuing westerly winds move the moisture further inland; therefore creating the wet season across this part of Africa (Miller et al., 2009). Nicholson (2009) also points to the importance of the African Easterly Jet and the Tropical Easterly Jet that dominate the dry

season, bringing warm dry air from the Sahara desert, through the Sahel region and into Nigeria. It is this wind that helps to maintain high temperatures and low humidity throughout the dry season. In addition it increases the amount of defuse aerosols (dust particles for examples) present in the atmosphere which help to form storm clouds once the rains have pushed in from the west (Miller et al., 2009).

The effect of this monsoon climate at the Kwano study site is that during periods of increased solar radiation (spring/summer) the mean maximum temperature is significantly reduced and mean minimum temperature is significantly increased, and humidity is also significantly increased from that of the winter (dry season) months. The importance of the wet season to the increase or decrease in abundance of many of the dipteran families studied in this thesis has been discussed in several previous sections, additionally it was stated that it is not only that the rains start that triggers these changes in dipteran abundance it is also the resultant changes in environmental parameters and the secondary effects of resource availability that affect the spatial patterns of abundance.

With the global climate predicted to increase in temperature over the next 50 years resulting in changing weather systems and patterns, subsequent alterations to the timings of the rains will have a profound affect on both the abundance and spatial patterns of the diptean families. The timing of the rains in this region of West Africa depend on the balance between the Easterly winds, known locally as the Hammatan winds (African Easterly Jet and Tropical Easterly jet, see above) and the monsoon winds. Two possible future scenarios of weather patterns for this region have therefore been predicted.

With the monsoon winds controlled by rising sea surface temperature in the Gulf of Guinea, global increases in temperature could in fact create a longer wet season (predictive models by Vigaud et al. (2011) have shown this to be a strong possibility) which would

affect both the abundance and spatial patterns of dipteran families. Many of the Nematocera species (with the exception of the Mycetophilids) increase in abundance in the wet season; therefore a greater generational turnover could be seen throughout the year if the wet season was to be extended. Families such as the Culicidae and Ceratopogindae are disease vectors for both human and non human mammal species and other members of this suborder have parasitic and parasitoid larvae preying on floral and faunal hosts. Therefore the impacts of higher abundances of these families could have severe effects on both the faunal and floral community. The Cecidomyiidae change from a ground canopy dominant population to a homogenous population spread throughout the canopy in the wet season, this would mean that a higher proportion of leaf galls would be formed which may impact the ability of vegetation to produce new viable growth. However there are also positive affects of increased populations of many of these dipteran families. As Diptera replace dry season dominant pollinators (such as bees) (Gonzalez et al., 2009), wet season pollination rates could increase therefore mitigating the potential damage caused by increased vegetative parasite attacks.

Increases in temperature may also prolong the Hammatan winds lengthening the dry season yet creating a more intense wet season (Kunstmann and Jung, 2005). This would have the opposite effect on the Nematocera families mentioned above; however may increase the generational turnover of members of the Calyptrate group as their preference is for hot dry environmental conditions. Parasitoid species of the Tachinidae family could grow abundance which would have secondary effects on their host species (Lepidoptera for example (Stireman, 2008)). Others such as the dung and carrion feeding Muscidae and Sarcophagidae could also increase in abundance due to the lack of competition from their wet season counterparts (dung beetles for example). However the overall effect on nutrient cycling rates over the cause of the year (as with pollination rates in the opposite scenario) may not change.

Toledo et al. (2011) predicted that increases in temperature and availability of water will increase tree growth rates in established tropical forests (logged forest growth rates only increase initially then the effect disappeared after 6 years); therefore in this tropical region of West Africa the forests themselves could expand. This was confirmed by Zelazowski et al. (2011) who predicted that the humid tropical forest niche around the Congo Basin (Kwano and the Gashaka Gumti National Park are situated on the periphery of this basin) could increase and therefore expand the available habitat for tropical humid forests to exist.

The exact effect of these changes in dipteran abundance and spatial patterns on the ecosystem can at this point only be projected based on the numerous climate prediction models and scenarios that are currently being investigated. What is evident, however, is that there will be distinct niche shifts within the ecosystem, modifications in the services that individual organisms provide to that ecosystem and changes in community structures for both the Diptera and other arthropods.

7.6 Final conclusions

Community ecology is a bottom up approach that indicates that the abundance, richness and diversity of species are driven by the availability of habitat resources (reproduction, egg laying medium, larval developmental habitat, emergence and feeding for example) and the effects of macro and microclimate on individual organisms (Loreau, 2010, Massol et al., 2011).

This thesis has explicitly shown that through the causes of spatial segregation due to forest structure and distance from the edge, environmental parameters, and life history traits, we

can map out the abundance of many families of Diptera within the habitat. This highlights the diverse nature of a tropical forest habitat, and the ever changing environment that you find within it. Niche specialisation is an important part of that diversity, with so many competing organisms it is the only way in which they can all survive and prosper.

The results and discussions from this thesis have brought together research from across tropical ecology due to the interactions that the Diptera have with their habitat. What has been shown is that a combination of optimal environmental conditions coupled with available larval development substraight increases abundance, and that environmental conditions coupled with feeding resources can dictate where adults will be found within the structure of the forest. This emphasises the complicated network of niches which invertebrates inhabit within the tropical environment, which also proves how and why tropical systems are so diverse. This ability to survive within a narrow band of conditions is a way of decreasing competition with other similar species, which may have similar requirements in terms of resources but secure them from different sources. Therefore the tropical forest system can support a diverse range of organisms in perpetual balance.

The balance of trophic levels within the tropical forest system is, however, vulnerable. Increasing anthropogenic pressure can destabilise this balance decreasing niches to less sustainable levels. The removal of a single species of plant or animal from a tropical forest system can have far reaching effects, often it is only once that species has disappeared that the true impact on the habitat can be calculated (Morris et al., 2004).

In section 1.6 three research questions were asked; the first asked how the abundance of Diptera and Collembola changed through the vertical column and how seasonal changes in the environment contributed to this. This thesis has shown that a non optimum environment, dry season for the Nematocera for example, abundance is controlled by

available larval development substrate and that environmental conditions dictate the spatial patterns through the vertical column. Yet when there is an optimal environment for these families the major contributing factor to their spatial arrangement through the vertical column is dictated by the availability of resources (feeding resources for example) provided by that stratum. The second question asked how the application of anthropogenic savannah burning affected the spatial patterns and abundance of the studied taxa. There were noticeable affects, for example the difference in forest density at the two sites that provided differences in environment, with dry season Calyptrate families, for example, preferring the hotter and dryer conditions that the burnt forest edge provided and the open hot, dry burnt savannah environment. Further more detailed study maybe needed in this area as the patterns that emerged are not wholly consistent, yet they are present. The third and final question asked what part the edge effects played in determining abundance and spatial patterns within the forest boundary. Here the determining factor of edge or core preference comes down to the environmental conditions found at the edge especially during the dry season when there is the most marked difference in microclimatic conditions between the forest edges and core.

This thesis has shown is that not only are those research question interlinked but also they are wholly dependent of the seasonality of the environment. The West African monsoon is responsible for the coming of the rains at a time where temperatures would be excessive. The monsoon winds reduce the temperature and increase humidity significantly as well as bringing much needed freshwater to areas that have been under drought conditions for several months. It is the first niche specialisation that these organisms seem to invoke. Division of season reduces competition not only with organisms within the same order but cross order competition also. This further enables a higher level of biodiversity to exist in the same space or be it not at the same time.

The results of this thesis have upheld the principles of community ecology theory, that of a bottom up approach where environment and resources dictated the abundance, richness and biodiversity of organisms within a habitat (Loreau, 2010), rather than a top down situation where predator and competition pressure limits these measurements. In this thesis environmental parameters and the availability of optimal larval development medium are dictating the overall abundance, environmental conditions are both suppressing or enhancing spatial patterns and the availability of feeding and reproductive resources are indicating where organisms are most abundant throughout the habitat. However at all times these are dependent on the season and the particular family's preference for certain environmental parameters. For example the Calyptrate family's spatial patterns are suppressed by the environment during the wet season as they prefer the dry season and visa versa for the Nematoceran families who prefer the wet season and are suppressed during the dry.

Shifting patterns in global weather and increases in global temperatures (even by a few degrees) can have consequences beyond what is obvious. Many of the families that have been investigated here are responsible for the pollination of specific plant species. Delays in the onset of the wet season, for example, would cause reductions in pollination rates, fruiting success and seed recruitment, all of which are relied on by plants, vertebrates and invertebrates. However an early start to the rains could increase the abundance of Diptera causing higher rates of infection in diseases, pathogens and parasites affecting human and non human populations. The narrow climatic and habitat niches in which tropical species inhabit are vulnerable, and we as humans have a responsibility to protect them.

Appendices

Appendix 1: Sample site locations in the Gashaka Gumti National Park.

Site	Co-ordinates	Sampling record		
		Tree Species	Total Dry	Total Wet
BT1	N7 19.575 E11 34.654	*Celtis zenkeri*	6	6
BT2	N7 19.561 E11 34.653	*Celtis zenkeri*	6	5
BT3	N7 19.557 E11 34.640	*Celtis zenkeri*	5	6
BT15	N7 19.670 E11 34.712	*Celtis zenkeri*	6	6
BT16	N7 19.650 E11 34.692	*Celtis zenkeri*	3	2
BT17	N7 19.674 E11 34.694	*Celtis zenkeri*	6	6
BT19	N7 19.674 E11 34.716	*Celtis zenkeri*	6	6
BT20	N7 19.677 E11 34.719	*Celtis zenkeri*	6	6
NBT4	N7 19.409 E11 34.734	*Celtis zenkeri*	3	0
NBT5	N7 19.396 E11 34.745	*Celtis zenkeri*	6	6
NBT7	N7 19.438 E11 34.729	*Celtis zenkeri*	5	6
NBT8	N7 19.451 E11 34.753	Mahogany *Sp.*	6	6
NBT21	N7 19.402 E11 34.830	*Celtis zenkeri*	3	0
NBT22	N7 19.329 E11 34.820	*Celtis zenkeri*	6	6
NBT23	N7 19.308 E11 34.824	*Celtis zenkeri*	6	6
NBT24	N7 19.305 E11 34.812	Mahogany *Sp.*	5	6
NBT25	N7 19.298 E11 34.804	Mahogany *Sp.*	3	6
I1	N7 19.743 E11 35.129	Mahogany *Sp.*	6	6
I2	N7 19.741 E11 35.130	*Celtis zenkeri*	3	0
I3	N7 19.760 E11 35.139	*Celtis zenkeri*	5	6
I4	N7 19.797 E11 35.151	*Celtis zenkeri*	5	6
I5	N7 19.858 E11 35.129		5	6

I6	N7 19.895 E11 35.152	*Celtis zenkeri*	3	5
I7	N7 19.865 E11 35.150	Mahogany *Sp.*	0	2
I8	N7 19.821 E11 35.185	Mahogany *Sp.*	0	6
I9	N7 19.786 E11 35.156	*Celtis zenkeri*	3	5
I10	N7 19.786 E11 35.134	*Celtis zenkeri*	3	6
BS1	N7 19.584 E11 34.726	N/A	2	1
BS2	N7 19.583 E11 34.726	N/A	2	1
BS3	N7 19.594 E11 34.721	N/A	2	1
BS4	N7 19.582 E11 34.718	N/A	2	1
BS5	N7 19.597 E11 34.722	N/A	2	1
BS6	N7 19.584 E11 34.709	N/A	2	1
BS7	N7 19.606 E11 34.722	N/A	2	1
BS8	N7 19.613 E11 34.714	N/A	2	1
NBS1	N7 19.370 E11 34.779	N/A	1	1
NBS2	N7 19.361 E11 34.783	N/A	1	1
NBS3	N7 19.371 E11 34.779	N/A	1	1
NBS4	N7 19.366 E11 34.779	N/A	1	1
NBS5	N7 19.376 E11 34.782	N/A	1	1
NBS6	N7 19.371 E11 34.787	N/A	1	1
NBS7	N7 19.378 E11 34.786	N/A	1	1
NBS8	N7 19.367 E11 34.791	N/A	1	1

BT = Burnt forest edge trees*
BS = Burnt savannah (inc. Pre and Post burn dry season)
I = Internal control plot trees*
NBS = Non burnt savannah
NBT = Non burnt forest edge trees*
* Tree sites include ground, mid and high canopy samples

Appendix 2: Dipteran families identified within samples

Nematocera*	Braychera*	Calyptrate†	Acalyptrate*
Bibionidae	Asilidae	Calliphoridae	Anthomyidae
Cecidomyiidae	Bombyliidae	Glossinidae	Chamaemyiidae
Ceratopogonidae	Dolichopdidae	Limoniidae	Chloropidae
Chironomidae	Empididae	Muscidae	Cryptochetidae
Culicidae	Phoridae	Rhiniidae	Drosophilidae
Lestremiinae	Pipunculidae	Sarcophagidae	Ephydridae
Mycetophilidae	Stratiomyidae	Tachinidae	Lauxaniidae
Psychodidae	Syrphidae	Tephritidae	Lonchaeidae
Scatopsidae	Tabanidae		Micropezidae
Sciaridae	Therevidae		Otitidae
Simuliidae			Piophilidae
Tipulidae			Platystomatidae
			Psilidae
			Pyrgotidae
			Sciomyzidae
			Sepsidae
			Sphaeroceridae
			Tephritidae

* Identified by D. Weaver using McAlpine (1983)
† Identified by N. Wyatt, Natural History Museum, London

Appendix 3: Calyptrate Species identification

Calliphoridae	Glossinidae	Limoniidae	Muscidae	Rhiniidae	Sarcophagidae	Tachinidae	Tephritidae
Chrysomya marginalis	Glossina fuscipes	Limoniidae sp.	Atherigona	Rhynchomya	Senotainia	Aplomya	Tephritidae sp.
Hemigymnochaeta gracilis	Glossina longipalpis		Brontaea			Blepharella (metalic sp.)	
Hemigymnochaeta unicolor	Glossina sp.		Coeaosia			Genus near Carcelia	
Hemigymnochaeta sp.			Hennigmyia			Carcelia ?aureiventris	
Phumosia pseudolucilia			Musca conducens			Ceromya	
Tricyclea perpendicularis			Musca lusoria			Chetogena	
Tricyclea (black thorax)			Musca sorbens			Chetogena (metallic green)	
			Musca sp.			Compsilura	
			Pectiniseta			Linnaemya	
			Phaoina ?varians			Mintho	
			Phaoina			Palexorista	
			Pygophora alemella			Peribaea	
			Pygophora parvipuncta			Blondeliini (sub Family)	
			Pygophora sp.			Eryciini (sub Family)	
			Pyrellina distincta			Exorista	
			Pyrellina sp.				
			Stomoxys pallidus				

All identification by N. Wyatt, Natural History Museum, London

Appendix 4: Raw data

Appendix 4a: Environmental and total abundance data

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Rain (mm)	Total Diptera abundance	Total Collembola abundance
BT	1	05/02/2009	49	0	Burnt Edge	0	32	0
BT	3	06/02/2009	38	0	Burnt Edge	0	24	0
BT	15	07/02/2009	13	0	Burnt Edge	0	21	0
BT	16	08/02/2009	23	0	Burnt Edge	0	24	0
BT	17	08/02/2009	8	0	Burnt Edge	0	13	0
BT	15	10/02/2009	13	10	Burnt Edge	0	4	0
BT	15	10/02/2009	13	24	Burnt Edge	0	8	0
BT	2	11/02/2009	67	0	Burnt Edge	0	27	0
BT	16	11/02/2009	23	10	Burnt Edge	0	15	2
BT	16	11/02/2009	23	21	Burnt Edge	0	3	0
BT	17	12/02/2009	8	10	Burnt Edge	0	3	0
BT	17	12/02/2009	8	20	Burnt Edge	0	4	0
BT	19	13/02/2009	12	10	Burnt Edge	0	8	0
BT	19	13/02/2009	12	20	Burnt Edge	0	2	0
BT	20	14/02/2009	8	0	Burnt Edge	0	12	1
BT	19	14/02/2009	12	0	Burnt Edge	0	16	0
BT	20	16/02/2009	8	8	Burnt Edge	0	6	0
BT	20	16/02/2009	8	18	Burnt Edge	0	2	0
BT	1	17/02/2009	49	10	Burnt Edge	0	11	0
BT	1	17/02/2009	49	18	Burnt Edge	0	3	0
BT	2	18/02/2009	67	10	Burnt Edge	0	4	0
BT	2	18/02/2009	67	22	Burnt Edge	0	5	0
BT	3	19/02/2009	38	10	Burnt Edge	0	3	0
BT	3	19/02/2009	38	21	Burnt Edge	0	12	0

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Rain (mm)	Total Diptera abundance	Total Collembola abundance
NBT	4	20/02/2009	29	10	Non Burnt Edge	0	3	0
NBT	4	20/02/2009	29	26	Non Burnt Edge	0	3	0
NBT	4	21/02/2009	29	0	Non Burnt Edge	0	11	0
NBT	5	22/02/2009	0	0	Non Burnt Edge	0	31	0
NBT	7	22/02/2009	46	0	Non Burnt Edge	0	21	0
NBT	5	24/02/2009	0	10	Non Burnt Edge	0	15	13
NBT	5	24/02/2009	0	21	Non Burnt Edge	0	1	3
NBT	7	26/02/2009	46	10	Non Burnt Edge	0	6	1
NBT	7	26/02/2009	46	22	Non Burnt Edge	0	14	1
NBT	8	02/03/2009	28	13	Non Burnt Edge	0	4	0
NBT	8	02/03/2009	28	28	Non Burnt Edge	0	16	0
NBT	21	03/03/2009	24	0	Non Burnt Edge	0	27	1
NBT	21	03/03/2009	24	10	Non Burnt Edge	0	14	5
NBT	21	03/03/2009	24	25	Non Burnt Edge	0	34	0
NBT	22	04/03/2009	24	10	Non Burnt Edge	0	3	0
NBT	22	04/03/2009	24	21	Non Burnt Edge	0	13	0
NBT	8	05/03/2009	28	0	Non Burnt Edge	0	47	4
NBT	22	05/03/2009	24	0	Non Burnt Edge	0	46	1
NBT	24	07/03/2009	48	0	Non Burnt Edge	12	16	4
NBT	24	08/03/2009	48	15	Non Burnt Edge	12.5	13	3
NBT	23	09/03/2009	28	0	Non Burnt Edge	0	44	0
NBT	23	09/03/2009	28	10	Non Burnt Edge	0	1	2
NBT	23	09/03/2009	28	25	Non Burnt Edge	0	18	0

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Rain (mm)	Total Diptera abundance	Total Collembola abundance
I	1	11/03/2009	177	0	Internal Control	0	59	2
I	2	11/03/2009	185	0	Intern v Control	0	23	4
I	1	13/03/2009	177	13	Internal Control	0	25	3
I	1	13/03/2009	177	20	Internal Control	0	22	9
I	2	16/03/2009	185	10	Internal Control	0	15	0
I	2	16/03/2009	185	20	Internal Control	0	15	0
I	3	17/03/2009	184	10	Internal Control	0	9	0
I	3	17/03/2009	184	25	Internal Control	0	15	0
I	4	18/03/2009	202	10	Internal Control	0	8	1
I	4	18/03/2009	202	20	Internal Control	0	8	0
I	5	19/03/2009	150	10	Internal Control	0	39	0
I	5	19/03/2009	150	21	Internal Control	0	63	0

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Rain (mm)	Total Diptera abundance	Total Collembola abundance
I	1	10/06/2009	177	0	Internal Control	1	0	0
I	1	10/06/2009	177	12	Internal Control	1	10	1
I	1	10/06/2009	177	26	Internal Control	1	17	4
I	3	11/06/2009	184	10	Internal Control	13	23	1
I	3	11/06/2009	184	23	Internal Control	13	13	0
I	4	12/06/2009	202	10	Internal Control	11	5	0
I	4	12/06/2009	202	22	Internal Control	11	9	0
I	3	13/06/2009	184	0	Internal Control	3	10	1
I	4	13/06/2009	202	0	Internal Control	3	4	0
I	5	14/06/2009	150	0	Internal Control	8	58	0
I	5	16/06/2009	150	10	Internal Control	14	10	4
I	5	16/06/2009	150	24	Internal Control	14	15	2
I	6	17/06/2009	202	10	Internal Control	26	9	0
I	6	17/06/2009	202	23	Internal Control	26	12	0
I	7	18/06/2009	206	10	Internal Control	8	11	0
I	7	18/06/2009	206	24	Internal Control	8	17	0
I	8	19/06/2009	263	0	Internal Control	2	10	1
I	8	21/06/2009	263	10	Internal Control	2	6	0
I	8	21/06/2009	263	30	Internal Control	2	27	0
I	9	23/06/2009	214	0	Internal Control	0	3	1
I	9	23/06/2009	214	10	Internal Control	0	10	1
I	10	24/06/2009	167	10	Internal Control	16	5	0
I	10	24/06/2009	167	21	Internal Control	16	17	2

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Rain (mm)	Total Diptera abundance	Total Collembola abundance
BT	15	26/06/2009	13	10	Burnt Edge	11	18	13
BT	15	26/06/2009	13	24	Burnt Edge	11	6	4
BT	19	02/07/2009	12	10	Burnt Edge	9	1	5
BT	19	02/07/2009	12	22	Burnt Edge	9	5	4
BT	20	03/07/2009	12	10	Burnt Edge	9	8	3
BT	20	04/07/2009	12	0	Burnt Edge	5	7	1
BT	15	05/07/2009	13	0	Burnt Edge	7	7	1
BT	19	05/07/2009	12	0	Burnt Edge	7	10	2
BT	20	05/07/2009	12	18	Burnt Edge	7	11	1
BT	17	06/07/2009	8	0	Burnt Edge	0	12	2
BT	16	07/07/2009	23	10	Burnt Edge	29	6	6
BT	16	07/07/2009	23	21	Burnt Edge	29	5	3
BT	17	08/07/2009	8	10	Burnt Edge	18	9	0
BT	17	08/07/2009	8	22	Burnt Edge	18	9	5
BT	1	09/07/2009	49	10	Burnt Edge	0	17	2
BT	1	09/07/2009	49	21	Burnt Edge	0	12	0
BT	2	10/07/2009	67	0	Burnt Edge	20	7	3
BT	1	11/07/2009	49	0	Burnt Edge	2	9	7
BT	3	12/07/2009	38	0	Burnt Edge	2	13	10
BT	2	13/07/2009	67	10	Burnt Edge	1	9	1
BT	3	14/07/2009	38	10	Burnt Edge	22	6	0
BT	3	14/07/2009	38	24	Burnt Edge	22	5	9

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Rain (mm)	Total Diptera abundance	Total Collembola abundance
NBT	8	15/07/2009	28	6	Non Burnt Edge	2	44	2
NBT	8	15/07/2009	28	29	Non Burnt Edge	2	39	6
NBT	7	16/07/2009	46	10	Non Burnt Edge	20	0	0
NBT	7	16/07/2009	46	26	Non Burnt Edge	20	8	1
NBT	5	17/07/2009	46	10	Non Burnt Edge	12	8	1
NBT	5	17/07/2009	46	26	Non Burnt Edge	12	10	6
NBT	5	18/07/2009	46	0	Non Burnt Edge	4	8	2
NBT	8	18/07/2009	28	0	Non Burnt Edge	4	15	2
NBT	7	19/07/2009	46	0	Non Burnt Edge	1	4	12
NBT	22	19/07/2009	24	0	Non Burnt Edge	1	18	6
NBT	23	20/07/2009	48	0	Non Burnt Edge	15	10	2
NBT	24	20/07/2009	28	0	Non Burnt Edge	15	17	3
NBT	22	21/07/2009	24	10	Non Burnt Edge	18	5	3
NBT	22	21/07/2009	24	21	Non Burnt Edge	18	20	8
NBT	24	22/07/2009	28	10	Non Burnt Edge	3	26	3
NBT	24	22/07/2009	28	26	Non Burnt Edge	3	43	0
NBT	25	22/07/2009	72	0	Non Burnt Edge	3	1	5
NBT	23	23/07/2009	48	10	Non Burnt Edge	0	21	2
NBT	23	23/07/2009	48	26	Non Burnt Edge	0	58	10
NBT	25	24/07/2009	72	28	Non Burnt Edge	2	17	3
NBT	26	24/07/2009	10	0	Non Burnt Edge	2	5	3
NBT	25	25/07/2009	72	10	Non Burnt Edge	7	14	0

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Min Temp °C	Max Temp °C	Min humidity %RH	Max humidity %RH	Rain (mm)	Total Diptera abundance	Total Collembola abundance
BT	20	23/03/2010	12	10	Burnt Edge	20	33	20	63	0	0	0
BT	20	23/03/2010	12	17	Burnt Edge	20	33	20	63	0	11	0
BT	19	24/03/2010	12	9	Burnt Edge	18	34	18	64	0	1	0
BT	19	24/03/2010	12	15	Burnt Edge	19	34	18	64	0	2	0
BT	15	25/03/2010	12	10	Burnt Edge	17	34	15	60	0	1	0
BT	15	25/03/2010	12	22	Burnt Edge	18	35	14	55	0	3	0
BT	17	26/03/2010	8	0	Burnt Edge	17	34	14	64	0	3	0
BT	17	26/03/2010	8	19	Burnt Edge	17	36	13	53	0	2	0
BT	15	27/03/2010	12	0	Burnt Edge	17	36	11	62	0	2	0
BT	17	27/03/2010	8	10	Burnt Edge	17	38	9	58	0	2	0
BT	19	28/03/2010	12	0	Burnt Edge	17	35	14	63	0	3	0
BT	20	28/03/2010	12	0	Burnt Edge	17	34	14	64	0	14	0
BT	1	29/03/2010	49	10	Burnt Edge	17	37	10	73	0	21	0
BT	1	29/03/2010	49	23	Burnt Edge	17	37	10	61	0	2	0
BT	2	30/03/2010	67	10	Burnt Edge	17	37	11	73	0	11	1
BT	2	30/03/2010	67	21	Burnt Edge	17	37	11	72	0	5	0
BT	3	31/03/2010	38	10	Burnt Edge	17	32	10	70	0	5	0
BT	1	02/04/2010	49	0	Burnt Edge	17	40	12	69	0	11	0
BT	2	03/04/2010	67	0	Burnt Edge	18	36	19	71	0	10	1

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Min Temp °C	Max Temp °C	Min humidity %RH	Max humidity %RH	Rain (mm)	Total Diptera abundance	Total Collembola abundance
NBT	8	01/04/2010	28	10	Non Burnt Edge	17	39	9	60	0	6	0
NBT	8	01/04/2010	28	28	Non Burnt Edge	19	40	9	51	0	4	0
NBT	8	02/04/2010	28	0	Non Burnt Edge	16	38	13	73	0	7	0
NBT	7	05/04/2010	46	10	Non Burnt Edge	17	38	19	72	0	2	0
NBT	7	05/04/2010	46	23	Non Burnt Edge	18	39	18	63	0	19	0
NBT	5	06/04/2010	46	10	Non Burnt Edge	19	40	22	83	0	1	1
NBT	5	06/04/2010	46	22	Non Burnt Edge	20	42	19	77	0	5	1
NBT	22	07/04/2010	24	10	Non Burnt Edge	22	36	28	84	0	0	0
NBT	22	07/04/2010	24	18	Non Burnt Edge	22	37	27	82	0	2	0
NBT	5	08/04/2010	46	0	Non Burnt Edge	21	33	50	100	1.5	2	2
NBT	22	08/04/2010	24	0	Non Burnt Edge	21	33	43	100	1.5	5	0
NBT	24	12/04/2010	28	0	Non Burnt Edge	22	34	38	95	0	2	1
NBT	24	12/04/2010	28	10	Non Burnt Edge	22	39	32	97	0	5	0
NBT	24	12/04/2010	28	22	Non Burnt Edge	24	36	38	87	0	0	0
NBT	25	13/04/2010	72	0	Non Burnt Edge	22	34	39	90	0	5	2
NBT	25	13/04/2010	72	10	Non Burnt Edge	22	36	29	90	0	3	0
NBT	25	13/04/2010	72	26	Non Burnt Edge	22	36	28	88	0	0	6
NBT	23	14/04/2010	48	0	Non Burnt Edge	21	34	46	100	1	3	0
NBT	23	14/04/2010	48	10	Non Burnt Edge	21	37	41	100	1	4	0
NBT	23	14/04/2010	48	23	Non Burnt Edge	21	37	41	100	1	5	0

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Min Temp °C	Max Temp °C	Min humidity %RH	Max humidity %RH	Rain (mm)	Total Diptera abundance	Total Collembola abundance
I	1	15/04/2010	177	0	Internal Control	22	32	52	100	30	12	1
I	1	15/04/2010	177	10	Internal Control	22	33	46	100	30	3	0
I	1	15/04/2010	177	25	Internal Control	22	33	46	100	30	2	0
I	3	20/04/2010	184	0	Internal Control	19	43	31	100	27	79	16
I	3	20/04/2010	184	10	Internal Control	19	44	32	100	27	56	21
I	3	20/04/2010	184	27	Internal Control	19	41	34	100	27	20	0
I	4	21/04/2010	202	0	Internal Control	20	33	47	100	32	156	1
I	4	21/04/2010	202	10	Internal Control	20	35	47	100	32	19	0
I	4	21/04/2010	202	24	Internal Control	20	36	43	100	32	11	0
I	5	23/04/2010	150	0	Internal Control	23	31	53	100	0	40	4
I	5	23/04/2010	150	10	Internal Control	23	32	49	97	0	26	5
I	5	23/04/2010	150	26	Internal Control	23	34	43	100	0	7	8
I	6	26/04/2010	202	0	Internal Control	21	31	57	100	49	75	2
I	6	26/04/2010	202	10	Internal Control	21	33	50	100	49	62	1
I	6	26/04/2010	202	21	Internal Control	21	33	50	100	49	55	1
I	9	29/04/2010	214	0	Internal Control	22	30	76	100	2	26	0
I	9	29/04/2010	214	10	Internal Control	22	34	52	100	2	55	0
I	9	29/04/2010	214	30	Internal Control	21	35	49	100	2	74	2
I	10	30/04/2010	167	0	Internal Control	22	26	21	100	4	24	0
I	10	30/04/2010	167	10	Internal Control	22	27	81	100	4	43	0
I	10	30/04/2010	167	23	Internal Control	22	27	78	100	4	22	2

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Min Temp °C	Max Temp °C	Min humidity %RH	Max humidity %RH	Rain (mm)	Total Diptera abundance	Total Collembola abundance
BT	20	19/05/2010	12	0	Burnt Edge	22	28	90	100	2	28	2
BT	20	19/05/2010	12	10	Burnt Edge	22	33	61	100	2	0	0
BT	20	19/05/2010	12	17	Burnt Edge	22	30	69	99	2	11	0
BT	19	20/05/2010	12	0	Burnt Edge	21	35	52	100	2	11	3
BT	19	20/05/2010	12	10	Burnt Edge	21	31	58	100	2	12	2
BT	19	20/05/2010	12	17	Burnt Edge	21	35	53	100	2	7	2
BT	15	24/05/2010	12	0	Burnt Edge	22	32	81	100	1	2	10
BT	15	24/05/2010	12	10	Burnt Edge	22	28	81	100	1	10	8
BT	15	24/05/2010	12	22	Burnt Edge	22	29	72	100	1	6	7
BT	17	25/05/2010	8	0	Burnt Edge	20	30	76	100	4	25	4
BT	17	25/05/2010	8	10	Burnt Edge	20	34	61	100	4	16	4
BT	17	25/05/2010	8	19	Burnt Edge	20	31	69	100	4	20	4
BT	1	26/05/2010	49	0	Burnt Edge	20	26	87	100	81	23	4
BT	1	26/05/2010	49	10	Burnt Edge	19	28	77	100	81	33	6
BT	1	26/05/2010	49	23	Burnt Edge	19	27	78	100	81	27	6
BT	2	27/05/2010	67	0	Burnt Edge	21	28	86	100	9	19	6
BT	2	27/05/2010	67	10	Burnt Edge	21	35	51	100	9	34	3
BT	2	27/05/2010	67	21	Burnt Edge	21	34	67	100	9	26	7
BT	3	31/05/2010	38	0	Burnt Edge	21	29	83	100	40	11	2
BT	3	31/05/2010	38	10	Burnt Edge	20	34	62	100	40	21	4
BT	3	31/05/2010	38	22	Burnt Edge	20	32	63	100	40	46	8

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Min Temp °C	Max Temp °C	Min humidity %RH	Max humidity %RH	Rain (mm)	Total Diptera abundance	Total Collembola abundance
NBT	8	01/06/2010	28	0	Non Burnt Edge	21	24	100	100	4	9	8
NBT	8	01/06/2010	28	10	Non Burnt Edge	21	26	80	100	4	41	6
NBT	8	01/06/2010	28	28	Non Burnt Edge	21	27	76	100	4	19	6
NBT	7	02/06/2010	46	0	Non Burnt Edge	21	26	91	100	21	13	3
NBT	7	02/06/2010	46	10	Non Burnt Edge	21	30	69	100	21	25	2
NBT	7	02/06/2010	46	23	Non Burnt Edge	21	31	60	100	21	45	2
NBT	5	03/06/2010	46	0	Non Burnt Edge	20	25	100	100	10	7	4
NBT	5	03/06/2010	46	10	Non Burnt Edge	20	29	78	100	10	24	7
NBT	5	03/06/2010	46	22	Non Burnt Edge	20	28	73	100	10	33	1
NBT	22	04/06/2010	24	0	Non Burnt Edge	21	27	80	100	7	6	1
NBT	22	04/06/2010	24	10	Non Burnt Edge	21	28	75	100	7	18	2
NBT	22	04/06/2010	24	18	Non Burnt Edge	21	29	69	100	7	2	1
NBT	24	07/06/2010	28	0	Non Burnt Edge	20	27	83	100	0	8	8
NBT	24	07/06/2010	28	10	Non Burnt Edge	20	31	63	100	0	19	5
NBT	24	07/06/2010	28	22	Non Burnt Edge	20	33	51	100	0	21	5
NBT	25	08/06/2010	72	0	Non Burnt Edge	20	28	86	100	6	11	3
NBT	25	08/06/2010	72	10	Non Burnt Edge	20	30	68	100	6	31	1
NBT	25	08/06/2010	72	26	Non Burnt Edge	20	33	59	100	6	28	2
NBT	23	09/06/2010	48	0	Non Burnt Edge	20	27	88	100	19	3	3
NBT	23	09/06/2010	48	10	Non Burnt Edge	20	33	60	100	19	76	2
NBT	23	09/06/2010	48	23	Non Burnt Edge	20	36	53	100	19	61	4

Site	Tree	Date	Distance from edge (m)	Height within tree (m)	Treatment	Min Temp °C	Max Temp °C	Min humidity %RH	Max humidity %RH	Rain (mm)	Total Diptera abundance	Total Collembola abundance
I	1	10/06/2010	177	0	Internal Control	20	26	88	100	7	9	2
I	1	10/06/2010	177	10	Internal Control	20	29	67	100	7	25	6
I	1	10/06/2010	177	25	Internal Control	20	28	72	100	7	13	7
I	3	11/06/2010	184	0	Internal Control	19	29	80	100	4	12	4
I	3	11/06/2010	184	10	Internal Control	19	35	53	100	4	85	6
I	3	11/06/2010	184	27	Internal Control	19	30	65	100	4	33	2
I	4	14/06/2010	202	0	Internal Control	20	30	76	100	5	6	12
I	4	14/06/2010	202	10	Internal Control	20	30	70	100	5	16	3
I	4	14/06/2010	202	24	Internal Control	20	31	64	100	5	17	3
I	5	15/06/2010	150	0	Internal Control	21	29	74	100	0	16	3
I	5	15/06/2010	150	10	Internal Control	20	32	58	100	0	31	4
I	5	15/06/2010	150	25	Internal Control	21	36	54	100	0	15	0
I	6	16/06/2010	202	0	Internal Control	20	28	89	100	11	14	1
I	6	16/06/2010	202	10	Internal Control	20	29	72	100	11	40	0
I	6	16/06/2010	202	21	Internal Control	19	30	69	100	11	22	2
I	8	17/06/2010	263	0	Internal Control	19	32	70	100	1	19	2
I	8	17/06/2010	263	10	Internal Control	19	29	70	100	1	23	1
I	8	17/06/2010	263	25	Internal Control	18	41	38	100	1	62	10
I	10	18/06/2010	167	0	Internal Control	22	28	74	100	1	9	8
I	10	18/06/2010	167	10	Internal Control	22	39	40	100	1	100	1
I	10	18/06/2010	167	23	Internal Control	22	39	39	100	1	13	2
I	9	21/06/2010	214	0	Internal Control	22	35	61	100	2	4	2
I	9	21/06/2010	214	10	Internal Control	22	39	42	100	2	76	9
I	9	21/06/2010	214	30	Internal Control	22	39	54	100	2	37	5

Site	tree	Date	Distance from edge of savannah (m)	Treatment	Total Diptera Abundance	Total Collembola Abundance
BB	1	21/01/2009	0	Pre Burn Dry	32	0
BB	2	21/01/2009	10	Pre Burn Dry	23	1
BB	3	22/01/2009	20	Pre Burn Dry	47	2
BB	4	22/01/2009	30	Pre Burn Dry	35	0
BB	5	26/01/2009	0	Pre Burn Dry	39	0
BB	6	26/01/2009	10	Pre Burn Dry	27	0
BB	7	27/01/2009	20	Pre Burn Dry	18	0
BB	8	27/01/2009	30	Pre Burn Dry	20	0
NBS	1	28/01/2009	0	No Burn Dry	28	0
NBS	2	28/01/2009	10	No Burn Dry	77	0
NBS	3	29/01/2009	20	No Burn Dry	44	1
NBS	4	29/01/2009	30	No Burn Dry	42	0
NBS	5	29/01/2009	0	No Burn Dry	22	0
NBS	6	29/01/2009	10	No Burn Dry	37	0
NBS	7	31/01/2009	20	No Burn Dry	35	0
NBS	8	31/01/2009	30	No Burn Dry	75	0
AB	1	01/02/2009	0	Post Burn Dry	93	0
AB	2	01/02/2009	10	Post Burn Dry	10	0
AB	3	02/02/2009	20	Post Burn Dry	13	0
AB	6	03/02/2009	10	Post Burn Dry	36	0
AB	7	04/02/2009	20	Post Burn Dry	30	0
AB	8	04/02/2009	30	Post Burn Dry	23	0
AB	4	05/02/2009	30	Post Burn Dry	50	1
AB	5	03/05/2009	0	Post Burn Dry	48	0
NBS	3	27/06/2009	5	No Burn Wet	25	5
NBS	1	26/07/2009	0	No Burn Wet	29	6
NBS	2	26/07/2009	0	No Burn Wet	15	2
NBS	4	27/07/2009	5	No Burn Wet	18	4
NBS	5	29/07/2009	20	No Burn Wet	41	7
NBS	6	29/07/2009	20	No Burn Wet	14	7
NBS	7	30/07/2009	30	No Burn Wet	25	4
NBS	8	30/07/2009	30	No Burn Wet	3	5
BS	1	31/07/2009	0	Post Burn Wet	18	2
BS	2	31/07/2009	0	Post Burn Wet	8	2
BS	3	01/08/2009	5	Post Burn Wet	38	5
BS	4	01/08/2009	10	Post Burn Wet	11	3
BS	5	02/08/2009	20	Post Burn Wet	34	0

Appendix 4a: Abundance data selected for higher level analysis

Site	tree	sample height	season	Ceratopogonidae	Sciaridae	Mycetophilidae	Chironomidae	Cecidomyiidae	Sarcophagidae	Muscidae	Tachinidae	Calliphoridae	Phoridae	Total Nematocera	Total Calyptrate	Total Acalyptrate	Total Other Brachycera
BT	1	ground	Dry 2009	2	0	0	1	16	0	0	1	0	8	19	1	3	9
BT	1	mid	Dry 2009	1	0	0	0	2	1	1	1	1	0	3	4	4	0
BT	1	high	Dry 2009	0	0	0	0	1	0	0	0	0	0	1	1	0	1
BT	2	ground	Dry 2009	0	0	0	3	16	0	1	0	0	1	20	1	5	1
BT	2	mid	Dry 2009	0	0	0	0	1	0	1	0	0	0	1	1	1	1
BT	2	high	Dry 2009	0	0	1	0	1	0	0	0	0	0	3	0	2	0
BT	3	ground	Dry 2009	3	0	0	6	3	0	0	0	0	2	15	0	7	2
BT	3	mid	Dry 2009	0	0	0	0	0	0	0	0	0	0	3	0	0	0
BT	3	high	Dry 2009	0	0	0	1	1	0	2	1	2	0	3	7	2	0
BT	15	ground	Dry 2009	1	0	0	0	10	1	0	2	0	2	11	4	3	3
BT	15	mid	Dry 2009	0	0	0	1	3	0	0	2	0	0	4	0	0	0
BT	15	high	Dry 2009	0	0	0	1	3	1	0	0	0	1	5	1	1	1
BT	16	ground	Dry 2009	1	0	0	0	15	0	0	0	0	1	17	0	6	1
BT	16	mid	Dry 2009	0	0	0	0	13	0	0	0	0	0	13	0	2	0
BT	16	high	Dry 2009	1	0	0	0	1	0	0	0	0	0	2	0	1	0
BT	17	ground	Dry 2009	0	0	0	0	12	0	0	0	0	1	12	0	0	1
BT	17	mid	Dry 2009	0	0	0	0	2	0	0	0	0	1	2	0	0	1
BT	17	high	Dry 2009	0	0	0	0	1	1	0	0	0	0	2	1	1	0
BT	19	ground	Dry 2009	0	0	0	0	6	1	3	0	0	5	6	4	1	5
BT	19	mid	Dry 2009	0	0	0	0	6	0	1	0	0	1	6	1	0	1
BT	19	high	Dry 2009	0	0	0	0	0	1	0	0	1	0	0	2	0	0
BT	20	ground	Dry 2009	0	0	0	0	5	1	0	1	0	1	7	2	2	1
BT	20	mid	Dry 2009	0	0	0	0	1	0	0	0	0	2	1	0	2	3
BT	20	high	Dry 2009	0	0	0	0	0	0	0	0	0	1	0	0	1	1
NBT	4	ground	Dry 2009	0	0	0	1	1	1	0	0	0	2	2	1	3	5
NBT	4	mid	Dry 2009	0	0	0	1	0	0	0	0	0	1	2	0	0	1
NBT	4	high	Dry 2009	0	0	0	1	1	0	0	1	0	0	2	1	0	0
NBT	5	ground	Dry 2009	0	0	0	0	22	0	0	0	0	2	23	0	2	6
NBT	5	mid	Dry 2009	1	0	0	0	5	0	0	0	0	1	7	0	1	7
NBT	5	high	Dry 2009	0	0	0	0	0	0	0	0	0	0	0	0	1	0
NBT	7	ground	Dry 2009	2	0	0	0	4	0	4	0	0	0	9	0	5	2
NBT	7	mid	Dry 2009	0	0	0	1	1	0	0	0	1	0	4	1	1	0
NBT	7	high	Dry 2009	0	0	0	1	4	1	2	1	3	0	5	7	2	0
NBT	8	ground	Dry 2009	1	0	0	1	20	0	5	3	0	6	22	11	8	6
NBT	8	mid	Dry 2009	0	0	0	0	0	0	0	2	1	0	0	3	1	0
NBT	8	high	Dry 2009	0	0	0	0	10	0	1	0	0	2	10	1	3	2
NBT	21	ground	Dry 2009	1	1	0	2	6	0	4	1	0	9	11	5	2	9
NBT	21	mid	Dry 2009	1	0	0	0	7	1	0	0	1	1	8	2	3	1
NBT	21	high	Dry 2009	1	1	0	0	2	0	4	2	6	12	5	12	3	14
NBT	22	ground	Dry 2009	1	0	0	0	15	0	1	10	2	14	16	15	1	14
NBT	22	mid	Dry 2009	0	0	0	0	3	0	0	0	0	0	3	0	0	0
NBT	22	high	Dry 2009	0	0	0	0	10	0	0	0	0	2	10	0	1	2
NBT	23	ground	Dry 2009	2	0	0	0	19	0	1	6	0	6	23	9	2	10
NBT	23	mid	Dry 2009	0	0	0	0	1	0	0	0	0	0	1	0	0	0
NBT	23	high	Dry 2009	1	0	0	0	1	0	3	1	0	5	3	4	6	5
NBT	24	ground	Dry 2009	0	0	0	1	10	0	1	0	1	3	11	2	0	3
NBT	24	mid	Dry 2009	3	0	0	1	4	0	1	0	0	1	11	1	0	1
–	1	ground	Dry 2009	1	0	0	1	39	0	5	2	2	1	43	9	5	2
–	1	mid	Dry 2009	0	0	0	0	0	3	0	2	0	19	1	5	0	19
–	1	high	Dry 2009	0	0	0	0	3	7	0	0	0	11	3	7	1	11
–	2	ground	Dry 2009	0	0	0	0	18	0	0	1	0	0	19	1	0	3
–	2	mid	Dry 2009	0	0	0	0	13	0	0	0	0	0	14	0	1	0
–	2	high	Dry 2009	0	0	0	0	9	0	0	1	0	3	9	1	2	3
–	3	mid	Dry 2009	1	0	0	0	5	1	0	0	0	0	6	1	0	2
–	3	high	Dry 2009	0	0	0	0	1	0	2	2	0	5	4	4	2	5
–	4	mid	Dry 2009	0	0	3	0	5	0	0	0	0	0	8	0	0	0
–	4	high	Dry 2009	0	0	4	0	0	0	0	0	0	0	5	0	3	0
–	5	mid	Dry 2009	0	2	19	0	2	4	0	0	0	0	24	4	11	0
–	5	high	Dry 2009	0	2	48	0	8	0	0	0	0	1	62	0	0	1

Site	tree		season	Ceratopogonidae	Sciaridae	Mycetophilidae	Chironomidae	Cecidomyiidae	Sarcophagidae	Muscidae	Tachinidae	Calliphoridae	Phoridae	Total Nematocera	Total Calyptrate	Total Acalyptrate	Total Other Brachycera
BT	1	ground	Wet 2009	3	1	0	0	5	0	0	0	0	0	9	0	0	0
BT	1	mid	Wet 2009	0	0	0	1	12	0	1	0	0	1	15	1	0	1
BT	1	high	Wet 2009	0	0	0	2	8	0	0	0	0	1	10	0	1	1
BT	2	ground	Wet 2009	1	1	0	0	5	0	0	0	0	0	7	0	0	0
BT	2	mid	Wet 2009	0	1	2	0	4	0	0	0	0	1	8	0	0	1
BT	3	ground	Wet 2009	1	2	0	6	4	0	0	0	0	0	13	0	0	0
BT	3	mid	Wet 2009	2	0	0	0	2	0	0	0	0	0	5	0	1	0
BT	3	high	Wet 2009	1	0	0	1	1	0	0	0	0	0	3	0	2	0
BT	15	ground	Wet 2009	1	0	2	0	4	0	0	0	0	0	7	0	0	0
BT	15	mid	Wet 2009	2	3	2	0	8	0	0	0	0	0	17	0	1	0
BT	15	high	Wet 2009	0	0	0	1	4	0	0	0	0	0	5	0	0	1
BT	16	mid	Wet 2009	0	0	0	1	4	0	0	0	0	0	5	0	1	0
BT	16	high	Wet 2009	1	1	0	0	1	0	0	0	0	0	4	0	1	0
BT	17	ground	Wet 2009	0	0	1	1	9	0	0	0	0	0	11	0	1	0
BT	17	mid	Wet 2009	0	0	1	1	7	0	0	0	0	0	9	0	0	0
BT	17	high	Wet 2009	1	0	0	0	7	0	0	0	0	0	9	0	0	0
BT	19	ground	Wet 2009	0	0	0	3	6	0	0	0	0	0	9	0	1	0
BT	19	mid	Wet 2009	0	1	0	0	0	0	0	0	0	0	1	0	0	0
BT	19	high	Wet 2009	0	0	0	0	4	0	0	0	0	0	5	0	0	0
BT	20	ground	Wet 2009	0	1	1	0	2	0	0	0	0	0	4	0	3	0
BT	20	mid	Wet 2009	0	3	1	1	3	0	0	0	0	0	8	0	0	0
BT	20	high	Wet 2009	3	2	0	1	2	0	0	0	0	1	8	0	2	1
NBT	5	ground	Wet 2009	1	1	1	0	4	0	0	0	0	0	8	0	0	0
NBT	5	mid	Wet 2009	2	2	1	0	1	0	0	1	0	0	7	1	0	0
NBT	5	high	Wet 2009	2	3	0	1	2	0	0	0	0	0	8	0	2	0
NBT	7	ground	Wet 2009	0	0	0	0	3	0	0	0	0	0	3	0	0	1
NBT	7	mid	Wet 2009	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NBT	7	high	Wet 2009	4	1	0	2	1	0	0	0	0	0	8	0	0	0
NBT	8	ground	Wet 2009	4	2	0	2	4	0	0	0	0	1	12	1	1	1
NBT	8	mid	Wet 2009	20	3	1	7	6	0	0	0	0	0	43	0	1	0
NBT	8	high	Wet 2009	6	11	0	4	13	0	0	0	0	1	37	0	1	1
NBT	22	ground	Wet 2009	2	7	1	2	2	0	0	0	0	0	16	1	1	0
NBT	22	mid	Wet 2009	2	1	1	0	1	0	0	0	0	0	5	0	0	0
NBT	22	high	Wet 2009	2	7	0	0	6	0	0	0	0	0	19	0	0	1
NBT	23	ground	Wet 2009	0	2	0	2	5	0	0	0	0	1	9	0	0	1
NBT	23	mid	Wet 2009	18	0	0	0	2	0	0	0	0	0	20	0	0	1
NBT	23	high	Wet 2009	8	8	0	12	22	0	0	0	0	3	54	0	1	3
NBT	24	ground	Wet 2009	0	2	1	0	11	0	0	0	0	1	15	0	1	1
NBT	24	mid	Wet 2009	26	0	0	0	0	0	0	0	0	0	26	0	0	0
NBT	24	high	Wet 2009	0	8	0	0	26	0	0	0	0	3	39	0	1	3
NBT	25	ground	Wet 2009	0	0	0	0	0	0	0	0	0	0	1	0	0	0
NBT	25	mid	Wet 2009	6	0	0	0	3	0	0	0	0	0	13	0	1	0
NBT	25	high	Wet 2009	1	1	0	4	4	1	0	0	0	1	15	1	0	1
NBT	26	ground	Wet 2009	0	1	1	0	3	0	0	0	0	0	5	0	0	0
I	1	ground	Wet 2009	0	0	0	0	0	0	0	0	0	0	0	0	0	0
I	1	mid	Wet 2009	2	0	0	0	1	0	0	0	0	0	8	0	2	0
I	1	high	Wet 2009	0	1	1	0	7	0	0	2	0	3	11	2	0	4
I	3	ground	Wet 2009	3	0	0	0	1	0	0	0	0	0	6	0	4	0
I	3	mid	Wet 2009	3	11	0	1	2	0	0	0	0	0	22	0	1	0
I	3	high	Wet 2009	0	3	0	3	0	0	0	0	0	1	8	1	3	1
I	4	ground	Wet 2009	0	1	0	0	1	0	0	0	0	1	2	0	1	1
I	4	mid	Wet 2009	1	0	0	0	1	0	0	0	0	0	5	0	0	0
I	4	high	Wet 2009	2	3	0	0	1	0	0	0	0	0	8	0	1	0
I	5	ground	Wet 2009	0	1	1	6	37	1	0	0	0	0	55	1	2	0
I	5	mid	Wet 2009	7	1	0	1	0	0	0	0	0	0	10	0	0	0
I	5	high	Wet 2009	0	3	0	1	5	0	0	0	0	2	11	0	2	2
I	6	mid	Wet 2009	1	0	0	0	1	0	0	0	0	3	4	0	2	3
I	6	high	Wet 2009	0	1	0	0	4	0	0	0	0	3	7	0	2	3
I	7	mid	Wet 2009	3	2	0	1	1	0	0	0	0	0	9	0	2	0
I	7	high	Wet 2009	1	3	0	2	10	0	0	0	0	0	16	0	1	0
I	8	ground	Wet 2009	0	2	0	1	4	0	0	0	0	1	8	0	0	2
I	8	mid	Wet 2009	2	2	0	0	1	0	0	0	0	0	6	0	0	0
I	8	high	Wet 2009	0	12	0	2	4	0	0	0	0	3	22	0	2	3
I	9	ground	Wet 2009	2	0	0	0	1	0	0	0	0	0	3	0	0	0
I	9	mid	Wet 2009	0	1	0	0	0	0	0	0	0	1	4	1	4	1
I	10	mid	Wet 2009	1	1	0	0	2	0	0	0	0	0	4	0	1	0
I	10	high	Wet 2009	2	7	0	1	5	0	0	0	0	0	17	0	0	0

Site	tree		season	Ceratopogonidae	Sciaridae	Mycetophilidae	Chironomidae	Cecidomyiidae	Sarcophagidae	Muscidae	Tachinidae	Calliphoridae	Phoridae	Total Nematocera	Total Calyptrate	Total Acalyptrate	Total Other Brachycera
BT	1	ground	Dry 2010	0	0	0	0	7	0	1	0	0	0	8	1	0	2
BT	1	mid	Dry 2010	0	0	0	0	19	0	0	0	0	0	20	0	0	1
BT	1	high	Dry 2010	0	0	0	0	2	0	0	0	0	0	2	0	0	0
BT	2	ground	Dry 2010	0	0	0	0	7	0	0	0	0	0	7	0	3	0
BT	2	mid	Dry 2010	0	0	0	0	11	0	0	0	0	0	11	0	0	0
BT	2	high	Dry 2010	0	0	0	0	4	0	0	0	0	0	4	0	1	0
BT	3	mid	Dry 2010	0	0	0	0	5	0	0	0	0	2	5	0	1	2
BT	3	high	Dry 2010	1	0	0	0	4	0	0	0	0	0	5	0	0	0
BT	15	ground	Dry 2010	0	0	0	0	1	0	0	0	0	1	1	0	0	1
BT	15	mid	Dry 2010	0	0	0	0	1	0	0	0	0	0	1	0	0	0
BT	15	high	Dry 2010	0	0	0	0	2	0	0	1	0	0	2	1	0	0
BT	17	ground	Dry 2010	0	0	0	0	3	0	0	0	0	0	3	0	0	0
BT	17	mid	Dry 2010	0	0	0	0	2	0	0	0	0	0	2	0	0	0
BT	17	high	Dry 2010	0	0	0	0	1	1	0	0	0	0	1	1	0	0
BT	19	ground	Dry 2010	0	0	0	0	2	0	0	0	0	0	2	0	0	1
BT	19	mid	Dry 2010	0	0	0	0	0	0	0	0	0	1	0	0	0	1
BT	19	high	Dry 2010	1	0	0	0	1	0	0	0	0	0	2	0	0	0
BT	20	ground	Dry 2010	0	1	0	0	13	0	0	0	0	0	14	0	0	0
BT	20	mid	Dry 2010	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BT	20	high	Dry 2010	0	0	0	0	1	10	0	0	0	0	1	10	0	0
NBT	5	ground	Dry 2010	0	0	0	0	1	0	0	0	0	1	1	0	0	1
NBT	5	mid	Dry 2010	0	0	0	0	1	0	0	0	0	0	1	0	0	0
NBT	5	high	Dry 2010	1	0	0	0	0	3	0	0	0	0	1	3	1	0
NBT	7	mid	Dry 2010	0	0	0	0	2	0	0	0	0	0	2	0	0	0
NBT	7	high	Dry 2010	0	0	0	0	5	3	0	1	0	2	5	6	6	2
NBT	8	ground	Dry 2010	0	0	0	0	5	0	1	1	0	0	5	2	0	0
NBT	8	mid	Dry 2010	0	0	0	0	3	1	0	0	0	0	5	1	0	0
NBT	8	high	Dry 2010	0	0	0	0	3	0	0	0	0	1	3	0	0	1
NBT	22	ground	Dry 2010	0	0	0	0	3	0	1	0	0	0	3	1	1	0
NBT	22	mid	Dry 2010	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NBT	22	high	Dry 2010	0	0	0	0	1	0	0	0	0	0	1	1	0	0
NBT	23	ground	Dry 2010	0	0	0	0	3	0	0	0	0	0	3	0	0	0
NBT	23	mid	Dry 2010	0	0	0	0	2	0	0	1	0	1	2	1	0	1
NBT	23	high	Dry 2010	0	0	0	1	0	0	1	0	0	0	2	1	2	0
NBT	24	ground	Dry 2010	0	0	0	0	2	0	0	0	0	0	2	0	0	0
NBT	24	mid	Dry 2010	2	0	0	0	0	0	0	0	0	0	2	0	3	0
NBT	24	high	Dry 2010	0	0	0	0	0	0	0	0	0	0	0	0	0	0
NBT	25	ground	Dry 2010	0	0	0	0	4	0	0	0	0	1	4	0	0	1
NBT	25	mid	Dry 2010	0	0	0	0	1	0	0	1	0	1	1	1	0	1
NBT	25	high	Dry 2010	0	0	0	0	0	0	0	0	0	0	0	0	0	0
I	1	ground	Dry 2010	0	0	0	1	2	0	0	1	0	3	3	1	2	6
I	1	mid	Dry 2010	0	0	0	0	2	0	0	0	0	0	2	0	1	0
I	1	high	Dry 2010	0	0	0	0	0	0	0	0	0	0	0	0	1	1
I	3	ground	Dry 2010	0	1	2	53	14	0	0	0	0	1	76	0	1	2
I	3	mid	Dry 2010	0	1	0	33	12	0	0	1	1	4	46	3	1	6
I	3	high	Dry 2010	0	0	0	10	7	0	0	0	0	1	17	0	2	1
I	4	ground	Dry 2010	0	2	1	125	24	0	0	1	0	0	154	1	1	0
I	4	mid	Dry 2010	0	0	3	11	4	0	0	0	0	0	18	1	0	0
I	4	high	Dry 2010	0	0	1	9	1	0	0	0	0	0	11	0	0	0
I	5	ground	Dry 2010	0	4	1	24	7	0	0	0	0	1	37	0	2	1
I	5	mid	Dry 2010	1	4	2	13	4	0	0	0	0	0	25	0	0	1
I	5	high	Dry 2010	0	0	0	5	2	0	0	0	0	0	7	0	0	0
I	6	ground	Dry 2010	0	12	7	13	41	0	0	0	0	0	74	0	1	0
I	6	mid	Dry 2010	0	27	6	10	13	0	0	0	0	0	59	0	2	1
I	6	high	Dry 2010	2	9	1	20	21	0	0	0	0	1	53	0	0	2
I	9	ground	Dry 2010	0	5	1	2	15	0	0	0	0	0	26	0	0	0
I	9	mid	Dry 2010	2	13	4	10	15	0	0	0	0	0	50	0	5	0
I	9	high	Dry 2010	1	11	0	27	28	0	0	1	0	1	71	1	1	1
I	10	ground	Dry 2010	2	1	3	6	12	0	0	0	0	0	24	0	0	0
I	10	mid	Dry 2010	3	6	3	8	18	0	0	0	0	0	41	0	1	1
I	10	high	Dry 2010	0	0	5	5	6	0	0	0	0	0	19	0	3	0

Site	tree		season	Ceratopogonidae	Sciaridae	Mycetophilidae	Chironomidae	Cecidomyiidae	Sarcophagidae	Muscidae	Tachinidae	Calliphoridae	Phoridae	Total Nematocera	Total Calyptrate	Total Acalyptrate	Total Other Brachycera
BT	1	ground	Wet 2010	0	4	0	0	19	0	0	0	0	0	23	0	0	0
BT	1	mid	Wet 2010	1	2	0	2	19	0	1	0	0	2	28	1	1	3
BT	1	high	Wet 2010	1	3	0	5	10	0	0	0	0	2	19	2	4	2
BT	2	ground	Wet 2010	2	2	2	1	10	0	0	0	0	0	19	0	0	0
BT	2	mid	Wet 2010	0	2	0	3	12	0	0	4	0	0	27	5	1	1
BT	2	high	Wet 2010	4	0	0	6	11	2	0	0	0	1	21	2	1	2
BT	3	ground	Wet 2010	8	0	0	0	2	0	0	0	0	0	11	0	0	0
BT	3	mid	Wet 2010	3	0	0	2	11	0	0	0	0	1	20	0	0	1
BT	3	high	Wet 2010	0	7	0	6	31	0	0	0	0	0	45	0	0	1
BT	15	ground	Wet 2010	0	0	0	0	1	0	0	0	0	0	2	0	0	0
BT	15	mid	Wet 2010	0	0	0	0	7	0	0	0	0	0	9	0	1	0
BT	15	high	Wet 2010	0	0	0	0	3	0	0	1	0	2	3	1	0	2
BT	17	ground	Wet 2010	1	1	0	1	22	0	0	0	0	0	25	0	0	0
BT	17	mid	Wet 2010	0	0	0	4	11	0	0	0	0	0	16	0	0	0
BT	17	high	Wet 2010	1	3	0	0	13	0	0	1	0	0	18	1	0	1
BT	19	ground	Wet 2010	1	1	0	1	7	0	0	0	0	1	10	0	0	1
BT	19	mid	Wet 2010	0	2	0	1	4	0	0	0	0	3	7	0	0	5
BT	19	high	Wet 2010	0	0	0	0	2	0	0	0	0	1	2	0	2	3
BT	20	ground	Wet 2010	2	1	0	4	19	0	0	0	0	0	26	0	1	1
BT	20	mid	Wet 2010	0	0	0	0	0	0	0	0	0	0	0	0	0	0
BT	20	high	Wet 2010	1	0	0	0	9	0	0	0	0	0	11	0	0	0
NBT	5	ground	Wet 2010	1	0	2	2	2	0	0	0	0	0	7	0	0	0
NBT	5	mid	Wet 2010	3	1	0	1	15	0	0	0	0	2	20	0	0	4
NBT	5	high	Wet 2010	1	1	0	4	23	0	0	0	0	3	30	0	0	3
NBT	7	ground	Wet 2010	4	0	1	0	7	0	0	0	0	0	13	0	0	0
NBT	7	mid	Wet 2010	0	3	0	3	13	0	0	1	1	2	20	2	1	2
NBT	7	high	Wet 2010	5	3	1	9	20	0	0	1	0	1	39	2	2	2
NBT	8	ground	Wet 2010	1	0	0	0	8	0	0	0	0	0	9	0	0	0
NBT	8	mid	Wet 2010	1	1	0	3	34	0	0	0	0	0	41	0	0	0
NBT	8	high	Wet 2010	0	3	1	1	13	0	0	1	0	0	18	1	0	0
NBT	22	ground	Wet 2010	0	2	1	0	1	0	0	0	0	0	5	0	0	1
NBT	22	mid	Wet 2010	3	1	0	4	9	0	0	0	0	0	17	0	1	0
NBT	22	high	Wet 2010	0	1	0	0	0	0	0	0	0	0	1	0	0	1
NBT	23	ground	Wet 2010	0	0	0	0	3	0	0	0	0	0	3	0	0	0
NBT	23	mid	Wet 2010	4	2	1	25	35	0	0	1	0	2	71	1	0	4
NBT	23	high	Wet 2010	3	6	0	11	31	0	0	0	0	2	56	0	2	3
NBT	24	ground	Wet 2010	1	0	1	1	3	0	0	0	0	0	6	0	0	2
NBT	24	mid	Wet 2010	0	2	2	2	12	0	0	0	0	1	18	0	0	1
NBT	24	high	Wet 2010	0	2	0	8	8	0	0	0	0	0	19	0	2	0
NBT	25	ground	Wet 2010	0	0	0	0	4	0	0	0	0	1	8	1	1	1
NBT	25	mid	Wet 2010	2	0	0	4	20	0	0	1	0	1	29	1	0	1
NBT	25	high	Wet 2010	1	1	0	10	14	0	0	1	0	0	27	1	0	0
I	1	ground	Wet 2010	0	0	0	1	7	0	0	0	0	0	9	0	0	0
I	1	mid	Wet 2010	1	3	0	0	12	0	0	0	0	3	19	0	2	4
I	1	high	Wet 2010	0	0	0	3	7	0	0	0	0	1	10	0	2	1
I	3	ground	Wet 2010	0	1	0	1	10	0	0	0	0	0	12	0	0	0
I	3	mid	Wet 2010	5	6	1	13	40	0	0	0	1	4	70	1	5	9
I	3	high	Wet 2010	5	3	0	12	9	0	0	1	0	2	29	1	1	2
I	4	ground	Wet 2010	1	0	1	0	1	0	0	0	0	1	5	0	0	1
I	4	mid	Wet 2010	2	1	2	0	6	0	0	0	0	1	14	0	0	2
I	4	high	Wet 2010	1	3	0	4	7	0	0	0	0	1	16	0	0	1
I	5	ground	Wet 2010	3	0	1	0	11	0	0	0	0	0	16	0	0	0
I	5	mid	Wet 2010	2	0	0	8	18	1	0	0	0	1	29	1	0	1
I	5	high	Wet 2010	1	1	0	3	5	0	0	0	0	4	11	0	0	4
I	6	ground	Wet 2010	2	0	0	1	10	0	0	0	0	0	14	0	0	0
I	6	mid	Wet 2010	5	2	0	5	21	0	0	0	0	4	34	0	2	4
I	6	high	Wet 2010	1	4	0	8	7	0	0	0	0	0	20	0	1	1
I	8	ground	Wet 2010	2	1	0	1	12	0	0	0	0	1	16	0	2	1
I	8	mid	Wet 2010	9	0	0	0	9	0	0	0	0	2	19	0	2	2
I	8	high	Wet 2010	14	7	1	12	11	0	0	0	0	12	49	0	1	12
I	9	ground	Wet 2010	0	0	0	0	2	0	0	0	0	2	2	0	0	2
I	9	mid	Wet 2010	18	6	0	2	41	0	0	0	0	3	71	0	2	3
I	9	high	Wet 2010	18	5	0	0	7	0	0	0	0	2	32	0	2	3
I	10	ground	Wet 2010	0	0	0	0	9	0	0	0	0	0	9	0	0	0
I	10	mid	Wet 2010	7	4	0	12	73	0	0	0	0	1	99	0	0	1
I	10	high	Wet 2010	2	2	0	1	5	0	0	0	0	2	11	0	0	2

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